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Research History and Opportunities in the Luquillo Experimental Forest

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INTRODUCTION

Tropical forests account for about 50% of the world's total forest area and tropical countries have a total population of about one billion people. Today many of the tropical forests are being subjected to high rates of deforestation because of the increased demand for agricultural land and fuel by the increasing human population. Management of forest areas in many tropical countries is primitive. Yet, the most powerful way to curb destruction of forests is through the application of sound management principles. Our ability to manage tropical forests is hampered by lack of understanding of their structure and function. Unlike the situation in the temperate zone, there is little long-term ecological research tradition in the tropics, particularly in the New World tropics. Much research in the New World tropics has been short and scattered. A notable exception is the research history at the Luquillo Experimental Forest in Puerto Rico where scientists have been active since the end of the last century and a tradition of forestry research exists. For example, a literature compilation of forestry works in the island (Mosquera and Feheley 1983) yielded 1,357 entries.

The objective of this paper is to summarize major findings of the research activity in the Luquillo Experimental Forest. In the context of this review, research opportunities in this tropical environment will become evident.

GENERAL DESCRIPTION OF THE RESEARCH AREA

Puerto Rico, part of the Greater Antilles island chain, is located in the northeastern Caribbean (fig. 1). The Luquillo Experimental Forest is located in the northeast corner of the island (fig. 2). This Forest, established in 1956, is congruent with the Caribbean

National Forest. The Caribbean National Forest was proclaimed a forest reserve in 1903 and has been managed by the U.S. Forest Service since 1917. Some land in the present Caribbean National Forest was protected under the Spanish Crown as early as 1860. When Puerto Rico became part of the United States territory in 1898, about 5,018 hectares of forest land in the Luquillo Mountains were under the protection of the Spanish Crown. The area of the Forest has increased since 1930 to its present size of 11,330 ha. A summary of these and other highlights of forestry activity in Puerto Rico are given in table 1.

The Luquillo Experimental Forest, located in the Luquillo Mountains, has elevations ranging from about 100 m to 1,075 m above mean sea level. The highest peak in the range is El Toro with an elevation of 1,075 m and the second highest peak is El Yunque with an elevation of 1,065 m (fig. 3). Other peaks with an elevation of approximately 1,000 m or more are Pico del Este (1,050 m), Pico del Oeste (1,020 m), El Cacique (1,020 m), Los Picachos (968 m), Mount Britton (937 m), and La Mina (925 m). The topography of the Mountains is extremely dissected with steep upper slopes. The largest proportion of the Mountains (which include the Experimental Forest) lies within the 305 to 610 m range (46%) with only 3% of the Mountains above 915 m (table 2). The Mountains serve as the headwaters for six major rivers. Río Espiritu Santo, Río Grande de Loíza, Río Blanco, Río Mameyes, Río Fajardo, and the Río Sabana. These rivers provide water supply to over 200,000 people.

The Luquillo Experimental Forest mainly includes four life zones; subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest (fig. 4). In addition, a small tract of land in the southwest portion is within the subtropical moist forest life zone. The largest proportion of the Forest is in the lower montane wet forest life zone.

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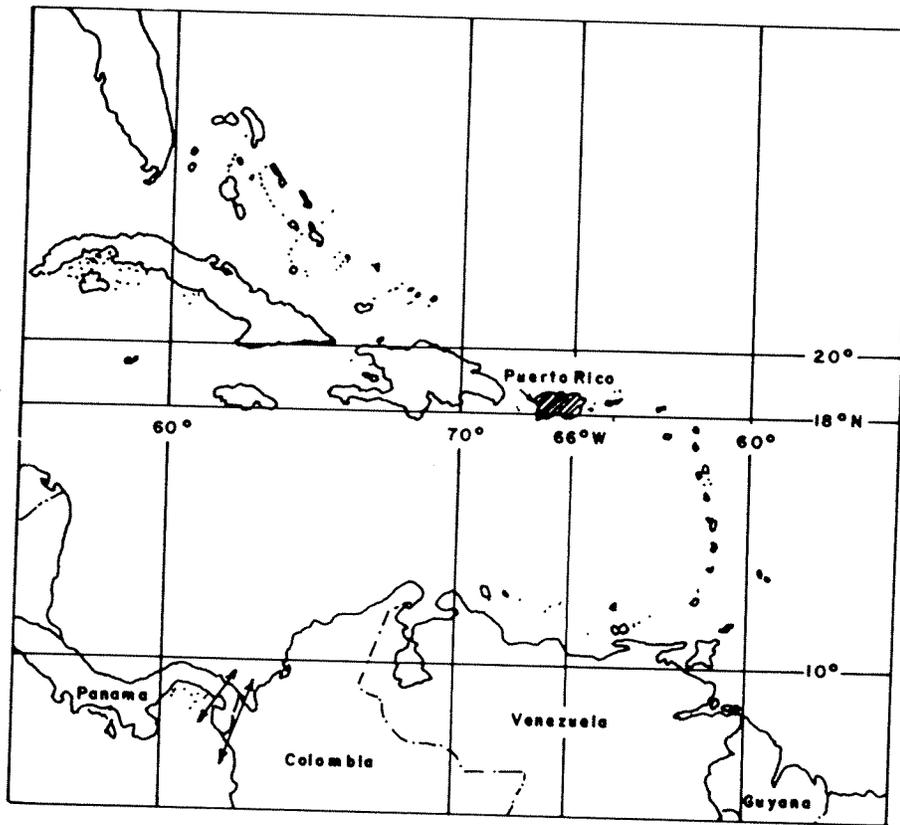


Figure 1.—Map of the Caribbean showing the location of Puerto Rico.

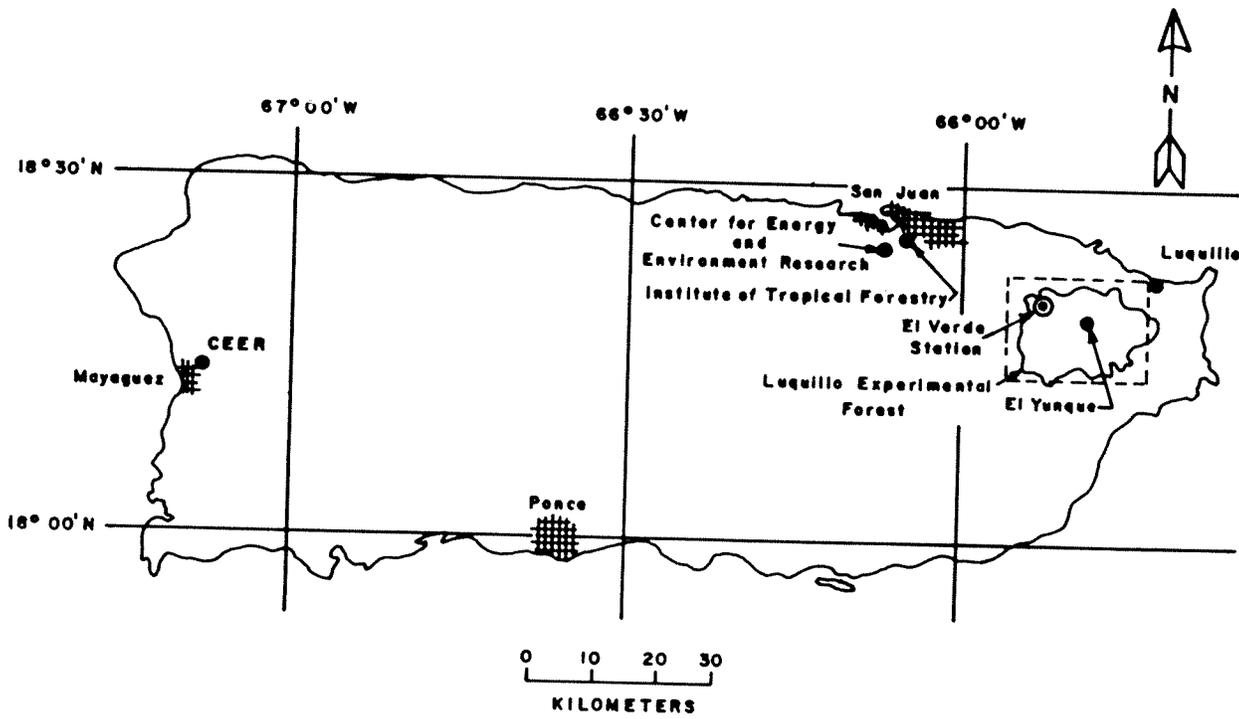


Figure 2.—Map of Puerto Rico showing the location of the Luquillo Experimental Forest.

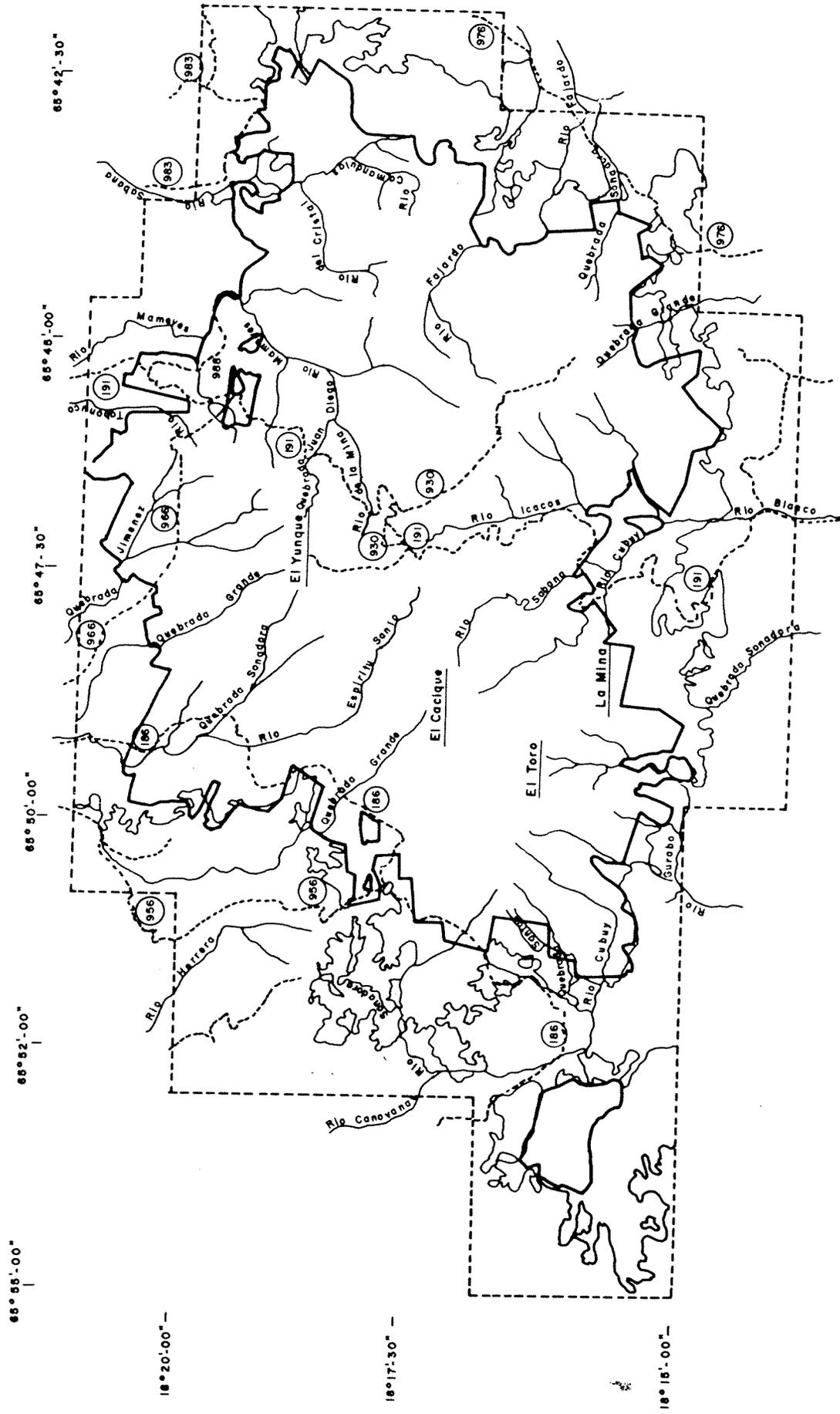


Figure 3.—Map of the Luquillo Experimental Forest.

Table 1.—Highlights of forestry in Puerto Rico (adapted from Mosquera and Feheley 1983)

1513	First Spanish law for Puerto Rico required tree planting on granted land.	1939	Tropical Forest Experiment Station (now Institute of Tropical Forestry) established in Puerto Rico. First of 24 volumes of <i>The Caribbean Forester</i> published.
1839	First Spanish forest conservation law for Puerto Rico.	1949	First timber management plan completed for the Caribbean National Forest.
1860	First Spanish public forestry appropriation for Puerto Rico.	1953	First of 18 international tropical forestry short courses held at the Institute of Tropical Forestry.
1876	Spanish proclamation of forest reserves in Puerto Rico.	1956	Cooperative forest management program began by Federal and State governments to intensify technical forestry assistance to private landowners, wood processors, and forest products consumers.
1898	Crown lands of Puerto Rico passed from Spain to the United States.	1956	Caribbean National Forest administratively designated also Luquillo Experimental Forest to foster research work there.
1903	U.S. proclaimed Luquillo Forest Reserve (now Caribbean National Forest).	1959	First successful establishment of Caribbean pine (<i>Pinus caribaea</i>) in Puerto Rico, now proven adaptable to much of the island.
1916	First boundary survey of Luquillo Forest completed area 5,035 ha.	1968	Formal research efforts to save the Puerto Rican parrot began in the Caribbean National Forest. Wild population has now increased from a low of 13 to about 30.
1917	First Supervisor of Luquillo Forest appointed. Insular (now Puerto Rico) Forest Service created by Puerto Rico government, placed under same Supervisor.	1973	Intensification of management of the Caribbean National Forest, with added professional personnel, accelerated silvicultural treatment of the forest, and visitor information services.
1918	Puerto Rico government reserved seven Insular (now State) Forests with an area of 13,600 ha.	1976	Luquillo Experimental Forest designated by the United States as part of the international network of Biosphere Reserves.
1920	Beginning of large-scale program of trial plantings with exotics and native tree species.	1977	Institute of Tropical Forestry transferred from the Office of the Chief of the U.S. Forest Service to the Southern Forest Experiment Station as its Tropical American Forest Management Research Unit.
1921	Insular Forest Service began program of tree distribution to landowners, continued to present.		
1931	Public purchase of lands for forestry begun in Puerto Rico. Total area now 39,200 ha.		
1933	Emergency Conservation Program began and with Civilian Conservation Corps program that succeeded it in 1937, accomplished extensive work in reforestation, forest road construction, and recreational and administrative improvements within both Federal and State Forests.		
1937	First timber inventory made of Caribbean National Forest.		

CURRENT LAND USE

Management

Although the terms Luquillo Experimental Forest and Caribbean National Forest (CNF) are applied to the same area of land, the objectives of the two groups that work in the forest are different. Management of the Forest comes under the auspices of the Caribbean National Forest, whereas research comes under the auspices of the Institute of Tropical Forestry. The principal objectives of the Caribbean National Forest are to make the lands as productive as possible and to demonstrate the results of forestry practices in a tropical environment. Research at the Institute suggested that about 6,700 ha of the Forest are capable of timber production and in the forest management plan of 1956 these were designated as commercial land. The majority of this land is located in the lower elevations of the Forest. Of this 6,700 ha of commercial forest land, about 2,750 ha

are active management, including management of natural stands and plantation development. The remaining 4,630 ha of forest land in the Luquillo Experimental Forest have been designated as noncommercial land, which is located on mountain peaks or on steep slopes and is dedicated to research and other miscellaneous uses.

Table 2.—Distribution of forest land area in the Luquillo Mountains by elevation (adapted from Wadsworth 1949)

Elevation above sea level (m)	Area (ha)	Percent of total area
122-305	5,091	26
305-610	9,106	46
610-915	4,897	25
915+	554	3
Total	19,648	100

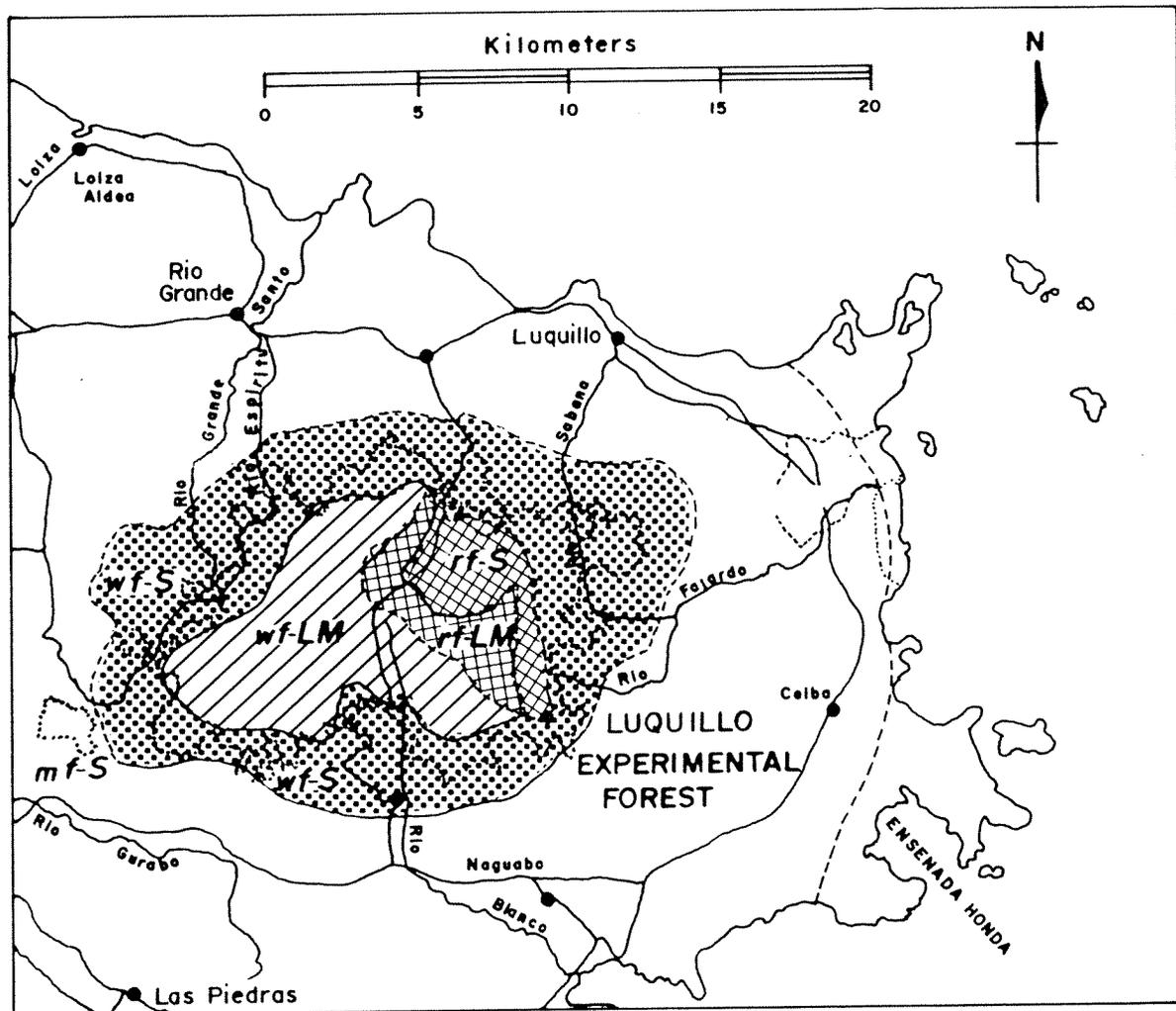


Figure 4.—Life zones in the Luquillo Experimental Forest (Ewel and Whitmore 1973). *mf-S* = subtropical moist forest; *wf-S* = subtropical wet forest; *rf-S* = subtropical rain forest; *wf-LM* = lower montane wet forest; *rf-LM* = lower montane rain forest. (--- = boundary of forest).

Research

To meet the objectives of the Institute of Tropical Forestry, specific areas of the forest have been designated for research use. Within the Luquillo Experimental Forest, different forest types grow on a variety of soil types and elevations, and under different intensities of rainfall and temperature (table 3). Most of the Luquillo Experimental Forest is old or cut-over colorado (*Cyrilla racemiflora*), palm (*Pretoea montana*), dwarf (also termed cloud, mossy or elfin forest), and second growth tabonuco (*Dacryodes excelsa*). Representative areas of the forest were identified as potential research sites in 1957 (table 4). By far, the largest research area is allocated for silvicultural activities (63%), followed by watershed studies (26%), plantations (6%), and reforestation studies (3%) (fig. 5).

Research tract "K" deserves special mention because it is also a *Research Natural Area* (RNA). This RNA, known as Baño de Oro, was established in 1949

by the U.S. Forest Service and is protected against any activities or use by the public that may directly or indirectly modify the natural environment. The objectives of the RNA are to preserve areas of land that represent as much as possible the major natural plant communities in an unmodified condition. They must also show evidence of no major disturbance by humans for at least 50 years. No physical improvements such as trails or roads are allowed in RNAs. However, temporary buildings and structures can be constructed to house such items as scientific instruments. The U.S. Forest Service encourages research compatible with the requirements outlined above.

The Baño de Oro RNA occupies 745 ha, of which about half is in the lower montane rain forest life zone and the other half is in the subtropical rain forest life zone. The vegetation types within the Baño de Oro are broken down as follows: 372 ha as tabonuco forest, 93 ha as colorado forest, 142 ha as palm forest, and 138 ha as dwarf forest.

In addition to the research tracts, there is a field

Table 3.—Areas of forest types and their condition on different sites in the Luquillo Experimental Forest (adapted from the 1951 Land Use Plan for the Forest)

Site	Approximate area by forest type and condition classes ^a					
	1	2	3	4	5	Total
-----ha-----						
Lower elevations (100–300 m)						
1. Deep acid clay soil	56	1,086	141	125	1,408
2. Shallow, slightly acid clay loam soil	8	4	12
3. Granitic loam soil	18	18
Medium elevations (300–600 m)						
4. Deep acid clay soil	1,076	59	2,072	150	76	3,433
5. Shallow, slightly acid clay soil	427	31	458
6. Granitic loam soil	34	37
Higher elevations (600–1,070 m)						
7. Valleys and gradual slopes, drainage impeded	3,399	3,399
8. Steep slopes and river courses, soils unstable	2,024	2,024
9. Peaks and exposed ridges	445	445
Total	1,132	5,927	3,593	378	201	11,231

- ^aThe forest type and condition classes represented in the Luquillo Experimental Forest are as follows:
1. *Old growth tabonuco forest.* With dominant trees of sawtimber species and quality, commonly more than 40.6 cm dbh (not necessarily virgin).
 2. *Colorado, palm, or dwarf forest.* Old or cutover forest composed almost entirely of trees which are neither at present nor potentially suited for sawtimber because of poor form, inferior wood, or small size at maturity.
 3. *Secondary tabonuco forest.* With dominant trees taller than 3m, generally of good form, some potentially of sawtimber quality but few or none mature for this purpose at present.
 4. *Plantations.* With the planted trees sufficiently represented to make up, potentially, 50% or more of the basal area.
 5. *Deforested.* Without vegetation taller than 3 m.

station at El Verde, on the northwestern slope of the Luquillo Experimental Forest, which occupies approximately 1 ha of fenced land inside a tabonuco forest (fig. 3). Built on the site of a former coffee plantation, the El Verde Field Station was used for a short while by the Civilian Conservation Corps who, in 1937, made surveys and did some timber cutting in the surrounding area. Until 1964 the station was used by the U.S. Forest Service as a field station. At that time, under an inter-agency agreement between the U.S. Atomic Energy Commission (presently the U.S. Department of Energy) and the Institute of Tropical Forestry, the station, as well as 69 ha of tabonuco forest in the immediate vicinity, were set aside for the Rain Forest Project of the Puerto Rico Nuclear Center under the direction of Howard T. Odum (see Odum and Pigeon 1970). Since then, the station has been the base of operations of the Terrestrial Ecology Division of the Center for Energy and Environmental Research (CEER).

Recreation

Approximately 264 ha of the Forest are allocated to the El Yunque Recreational Area located in the middle of the Luquillo Experimental Forest. This recreational area provides picnic shelters and foot trails to nearby peaks and other points of interest. Almost 2 million people (equivalent to about two-thirds of the total population of Puerto Rico) visit this area each year.

PROPOSED LAND USE

Existing and proposed land uses in the Luquillo Experimental Forest (1978 land use plan) are shown in figure 6. Baño de Oro RNA presently occupies approximately 745 ha. A proposal to expand this RNA to approximately 1,154 ha and to incorporate more area of the dwarf, colorado, and palm forests on dif-

Table 4.—Summary of reserved research tracts in the Luquillo Experimental Forest and their proposed use (adapted from the 1957 Land Use Plan). Refer to figure 6 for location of research tracts

Tract	Site ^a	Stand ^a condition	Approximate area (ha)	Proposed research use
A	5	3	113.3	Silviculture
	5	4	6.1	Plantation mgt.
			119.4	
B	4	3	87.4	Silviculture
	4	5	8.1	Reforestation
			95.5	
C	4	3	73.6	Silviculture
D	4	3	40.1	Silviculture
	4	5	12.5	Reforestation
			52.6	
E	1	3	12.1	Silviculture
	1	5	15.0	Reforestation
	4	4	52.2	Plantation mgt.
			79.3	
F	1	3	16.2	Silviculture
	1	5	30.0	Reforestation
	4	3	8.1	Silviculture
	4	4	8.1	Plantation mgt.
			62.4	
G	7	2	48.5	Silviculture
H	7	2	344.8	Watershed
	8	2	44.5	Watershed
	9	2	28.3	Watershed
			417.6	
I	1	3	36.4	Silviculture
	1	4	4.0	Plantation mgt.
	4	1	23.5	Silviculture
	4	2	52.2	Unassigned palm type
	4	3	12.1	Silviculture
			128.2	
J	1	3	48.5	Silviculture
	1	5	11.0	Reforestation
	2	4	4.0	Plantation mgt.
			63.5	
K	1	1	16.2	Silviculture
	4	1	463.8	Silviculture
	7	2	93.1	Silviculture
	8	2	141.6	Silviculture
	9	2	137.6	Silviculture
			852.3	
L	4	1	113.7	Silviculture
	4	3	18.2	Silviculture
			131.9	
M	4	1	85.8	Watershed
	4	3	144.1	Watershed
			229.9	
N	3	4	18.2	Plantation mgt.
	5	3	94.3	Silviculture
	5	4	24.7	Plantation mgt.
	6	4	33.6	Plantation mgt.
			170.8	
Total			2526	

^aRefer to table 3 for description.

ferent kinds of slopes and soils is under consideration. Another proposal would add the *El Cacique Research Natural Area*, about 595 ha, with The El Cacique peak in the center. The proposed El Cacique RNA includes many endemic species, some endangered plant species, and vegetation on soil types not included in the Baño de Oro RNA or its proposed extension.

In addition to the expansion of the RNAs, it is proposed that two areas be designated for watershed studies. The proposed watershed study areas are the same as those that have been reserved since 1957 (fig. 6). Other proposed research areas are similar to those that have been in use since 1957, except for some additions and deletions, which are summarized in table 5. The total amount of land proposed to be set aside for research use has increased from 2,344 ha in 1957 to the present area of 3,189 ha.

Superimposed on these proposed research areas are two other types of land use. One is the 3,116 ha pro-

Table 5.—Proposed land use allocation for research areas in the Luquillo Experimental Forest (Progress Report to J. Muñoz, Forest Supervisor, July 13, 1978)

Tract for research	1957	1978	Suggested studies ^a
	----- ha -----		
Tract 105	119.4	235.9	1-2
Tract 21	17.8	0	
Tract 16L	140.0	20.2	1-2
Tract 18	73.6	0	
Tract 14A	0	59.5	1-2
Research E&F	161.1	209.6	1-2
Sonadora	0	102.4	3
Research G	101.2	0	
Research H&I	128.3	66.4	3
Research L	132.0	159.4	3
Research N	33.6	33.6	1-2
Natural Areas			
Baño de Oro	744.6	1,154.2	3
Cacique	0	594.9	3
Watersheds			
Espiritu Santo	466.2	341.5	watershed
Camandulas/Sabana	229.0	229.8	watershed
Subtotals			
Natural forests	1,106.0	2,077.3	
Plantations	541.5	544.7	
Watersheds	696.1	571.4	
Total	2,343.6	3,189.4	

- ^a1. Studies on representative pine sites and in existing pine plantations.
2. Studies in plantations other than pine species.
3. Studies in naturally generated forests.

posed Critical Habitat of the endangered parrot *Amazona vittata*. The critical habitat, overlapping all research natural areas and one of the watershed research areas (fig. 6), is compatible with nondestructive research. The other proposed land use change for the Luquillo Experimental Forest is Roadless Area Review and Evaluation (RARE II) Program. The RARE II program is designed to provide balanced management of public lands to meet the nation's many needs. Wilderness areas selected from RARE II lands can only be created or declassified by an act of Congress. The proposed RARE II area of 3,938 ha in the Luquillo Experimental Forest would be called the El Cacique Wilderness Area, but the boundaries and the size of the actual wilderness area have not yet been determined. The proposed RARE II area overlaps the proposed El Cacique RNA, the watershed study area of the headwaters of the Río Espiritu Santo, and the proposed Critical Habitat Area for the parrot.

The RARE II Area, when designated as a wilderness area, will enable the public to have access to the region. However, no structures other than trails may be built within this wilderness area. Nondestructive research will be allowed within the RARE II area. Although no permanent research structure would be allowed, equipment such as weather stations, weirs, rain gages, and litter boxes would be allowed.

There are no current plans to expand the El Yunque Recreational Area. However, proposals are pending to enlarge a picnic area in the west near road 185 and to rebuild 191 at the southern end, which recently had large portions destroyed by landslides.

Rainfall

Weather stations are located within and adjacent to the Luquillo Experimental Forest (fig. 7). Patterns of annual rainfall for these stations from 1896 to the present are shown in figure 8. The earliest data were recorded for stations at 152 m and 366 m elevation at Hacienda Perla. Rainfall records are quite extensive for stations near the Forest from 1908 to the present, with the exception of two years (1951 and 1952) when records were not published. Rainfall appears to be quite variable from year to year.

The mean rainfall, coefficient of variation, and standard error of the mean for the period of record for each station shown in figure 8 is given in table 6. The stations are arranged according to elevation from the lowest (Río Blanco at 30.5 m) to the highest (Pico del Este at 1,051 m). Rainfall generally increased with elevation (fig. 9) up to approximately 700 m (La Mina) and then decreased at the higher elevation station (Pico del Este). Both La Mina and Pico del Este stations are in rain forest life zones (fig. 4) and their rainfall should be similar; however, the period of record at both was short (8–9 yr) and did not overlap. The mean annual rainfall ranged from approximately 245 cm/yr at lower elevations to approximately 400 cm/yr at higher elevations. Coefficients of variation, which show no definite trend in the variation of year-to-year annual rainfall range from a low of 15% for Río Blanco to a high of 39% at Pico del Este (table 6).

Table 6.—Station descriptions and their mean rainfall for stations within and adjacent to the Luquillo Experimental Forest

Station	Elevation (m)	Location lat/long °N/°W	Years of record	Mean rainfall (cm)	C.V. ^a (%)	S.E. ^b
Río Blanco 1	30.5	18° 15' / 65° 47'	12	246	15	11
Río Blanco 2a	40	18° 15' / 65° 47'	16	263	31	20
Paraiso	101	18° 16' / 65° 43'	43	233	19	7
Río Grande El Verde	107	18° 21' / 65° 49'	20	264	30	18
Río Grande El Verde	107	18° 21' / 65° 49'	21	267	28	16
Río Blanco 3	152	18° 15' / 65° 47'	18	268	23	15
El Verde	500		7	392	33	49
Río Blanco 4	549	18° 18' / 65° 47'	27	387	13	10
La Mina	716		8	470	19	32
Pico del Este	1,051	18° 16' / 65° 45'	9	360	38	46

^aCoefficient of variation (C.V.) = $\frac{\text{Standard deviation}}{\text{mean}} \times 100$

^bStandard error of the mean

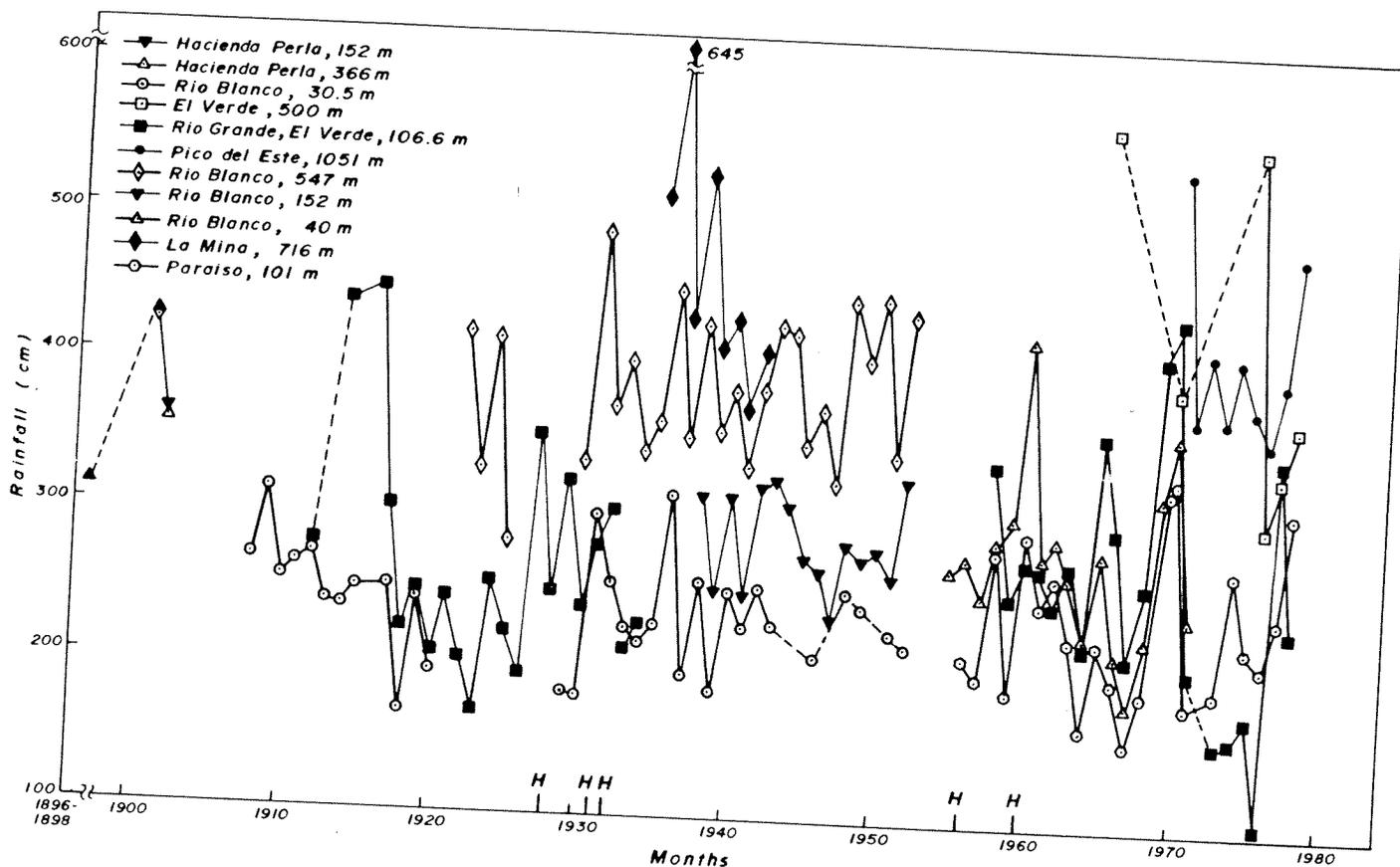


Figure 8.—Patterns of annual rainfall for stations in and adjacent to the Luquillo Experimental Forest (U.S. Department of Agriculture, 1909–1914, 1915–1921, 1921–1939; U.S. Department of Commerce, 1940–1952, 1955–1979, Wilson, 1899). Dates of hurricanes are indicated by an “H”.

Mean monthly rainfall and minimum and maximum rainfall for the period of record for each of the stations within and adjacent to the Forest are shown in figure 10. The annual totals in these figures are different from those in table 6 because table 6 was produced from data for complete years only, whereas figure 10 was produced from the means of all months with rainfall records including months from incomplete years. The stations are arranged according to elevation from the highest (Pico del Este; fig. 10a), to the lowest (Río Blanco; fig. 10i). In general, all stations show a similar annual pattern. Peak rainfall generally occurred in May, but it occurred in October in the highest elevation station (fig. 10a). The mean monthly rainfall varied from a low of 20 cm to a high of approximately 55 cm at Pico del Este (fig. 10a), and from a low of 15 cm to a high of 30 cm at Río Blanco (fig. 10i). Records from lower elevations generally showed a more uniform distribution of rainfall from April through November than records from higher elevations.

The total duration of rainfall, in hours, for a given month for the period 1939–1941 for La Mina station is shown in figure 11. In general, the longest duration of rainfall was during November to January, and June

coinciding with periods of low rainfall at this station (c.f. fig. 10b). This indicates that during these months storm events are longer but of low intensity (approximately 0.6–0.8 cm/hr). Short duration of rainfall occurred during July–October coinciding with higher rainfall (c.f. fig. 10b) and indicating intense storms (approximately 1.3 cm/hr).

Table 7 summarizes rainfall characteristics for La Mina station (adapted from Wadsworth 1949). During most rainy days, this station received about 0.03 cm of rainfall. Approximately 50 days out of the year received more than 2.54 cm of rainfall. Total duration of rainy weather in a year was approximately 22 days which represents about 6% of the year. Most of this rainfall tends to fall between the hours of 6:00 A.M. to 6:00 P.M. It is obvious that, although the Luquillo Experimental Forest receives a high rainfall, it actually rains for a relatively short period of time. In terms of duration, over 90% of the year is rain-free.

Temperature

Long-term temperature data for locations in and adjacent to the Luquillo Experimental Forest are quite limited (fig. 12). The earliest temperatures

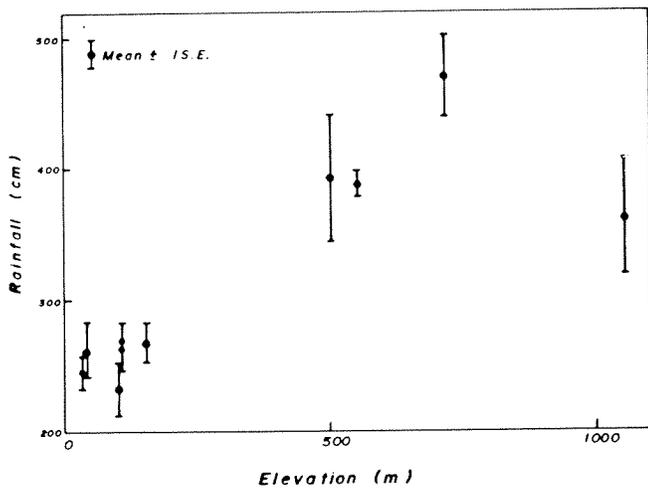


Figure 9.—Variation of mean annual rainfall with elevation. Data are from table 6.

Table 7.—Rainfall characteristics at La Mina (adapted from Wadsworth 1949)

Extreme minimum annual precipitation (cm)	373
Extreme maximum annual precipitation (cm)	645
Extreme maximum monthly precipitation (cm)	103
Extreme maximum daily precipitation (cm)	31
Number of days/year with at least:	
0.03 cm rainfall	269
0.64 cm rainfall	116
2.54 cm rainfall	53
Average number of showers/year	1,625
Average rainfall per shower (cm)	0.3
Average duration per shower (min)	19
Total annual rainfall duration: (days)	22
(% of year)	6.0
Average rainfall intensity (cm/hr)	0.8
Rainfall duration per rainy day (hr)	1.8
Days per year with more than one hour of rain	156
Maximum intensities (cm)	
5 min	1.6
20 min	3.7
60 min	6.5
120 min	8.3
Per cent of total rainfall from 6 A.M. to 6 P.M.	55

were measured at Hacienda Perla where the mean annual temperature was approximately 25°C. Mean annual temperature decreased from low to high elevation stations (fig. 12). The year-to-year variation in temperature appears to be quite small.

Mean monthly, maximum and minimum temperatures in the Luquillo Experimental Forest are shown in figure 13. Sharp decreases in mean monthly temperature occurred from low to high elevation stations. There was a 7°C difference between the mean maximum temperature for the lowland and upland stations. The temperature range in any given month at

lower elevations was larger than at higher elevations. The annual variation in the mean monthly temperature was similar for low and high elevation stations (3.5°C and 3°C, respectively).

Data on many climatic variables for stations within and adjacent to the Luquillo Experimental Forest (fig. 14 and table 8) were collected on an hourly basis for the period 1958–1962 (Briscoe 1966). Temperature and relative humidity data were collected for all the stations shown in figure 14; other climatic data, such as rainfall, wind direction, wind speed, and solar radiation, were collected only at a few of these stations. Briscoe's original publication presented only the raw data.

Mean monthly temperatures for the stations used in Briscoe's (1966) study followed the same trends as those stations shown in figure 13 (fig. 15). The September temperature for Catalina station (fig. 15) appears to be anomalous when compared to the data for the other stations.

Diurnal variation in temperature for high elevation stations was less than that for low elevation stations (fig. 16). For example, at El Yunque the diurnal variation was approximately 1.5°C and at the lowest elevation station, Río Blanco, the diurnal variation was approximately 6.5°C. Maximum temperature at El Yunque occurred approximately at noon, whereas at lower elevations the maximum daily temperature occurred approximately 1 hr later. Diurnal variation in temperature in June at all stations was approximately the same as it was in January (fig. 16b). However, maximum daily temperature in June at El Yunque occurred 1–2 hrs later than in January. The maximum daily temperature in June for the low elevation stations occurred at the same time as it did in January.

Temperature profile measurements at heights ranging from 400 cm above ground surface to a soil depth of 25 cm were available only for the El Yunque station (fig. 17). The anomalies in the data for April and June are probably errors in the original data. In general, temperatures increased from a height of 400 cm above ground surface to a depth of 25 cm below ground surface. Soil temperatures at the three depths of 2.5, 7.5 and 25 cm were very similar to each other and were higher than all the temperatures measured at surface and above in any given month.

Relative Humidity

The annual course in relative humidity for the high elevation station at El Yunque shows a fairly uniform humidity of approximately 98% (fig. 18). The most western station of all those shown in figure 14, Cubuy, had the lowest relative humidity and also the

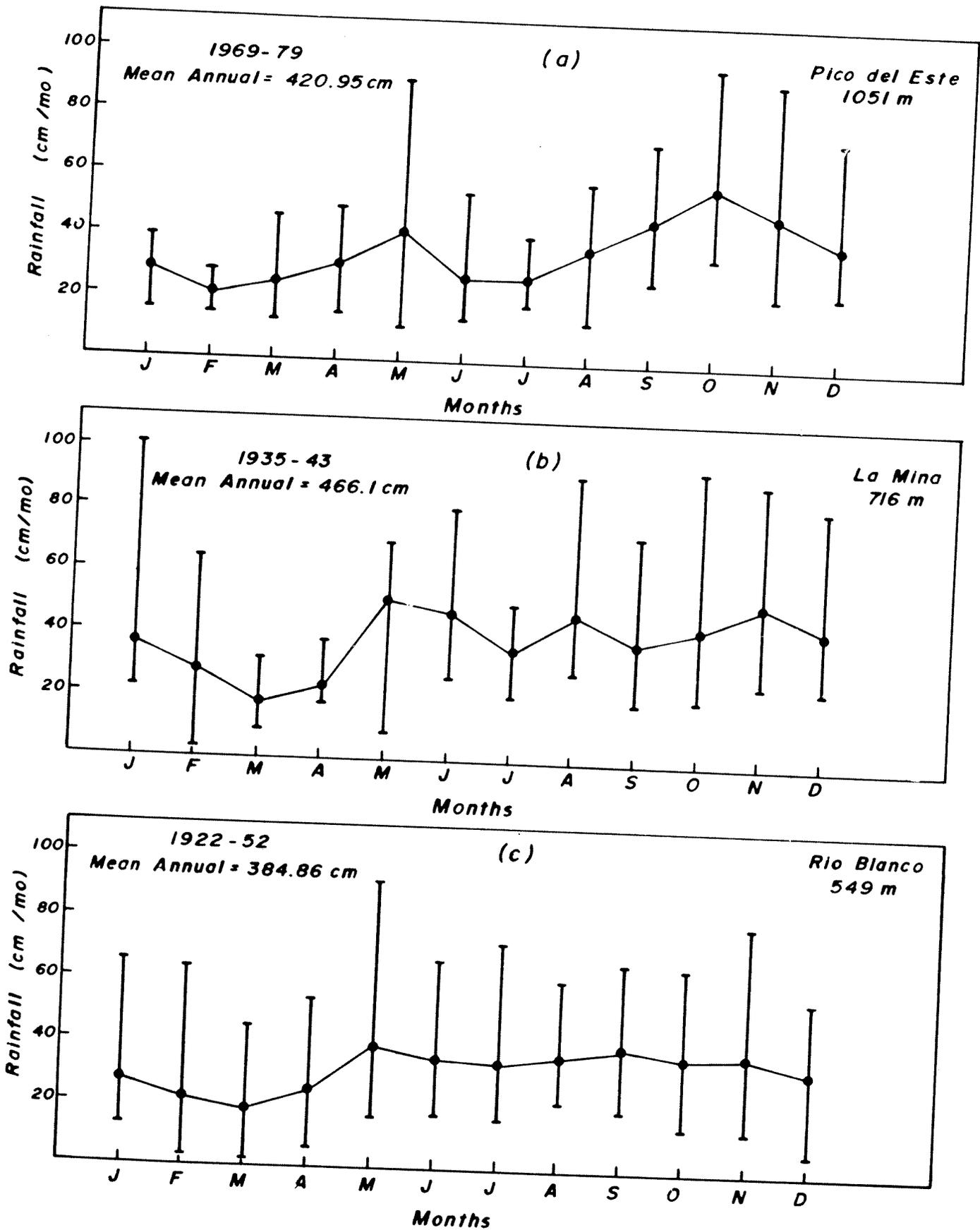


Figure 10.—Maximum, minimum, and mean monthly rainfall for stations in and adjacent to the Luquillo Experimental Forest (data from U.S. Department of Agriculture, 1909-1914, 1915-1921, 1921-1939; U.S. Department of Commerce, 1940-1952, 1955-1979).

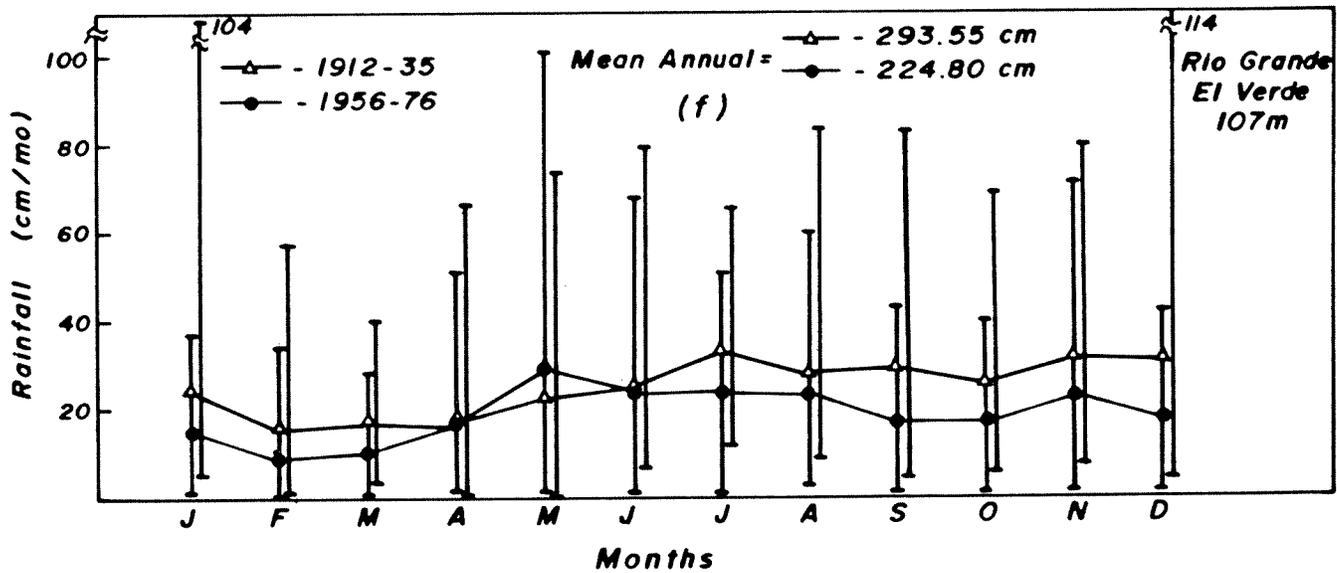
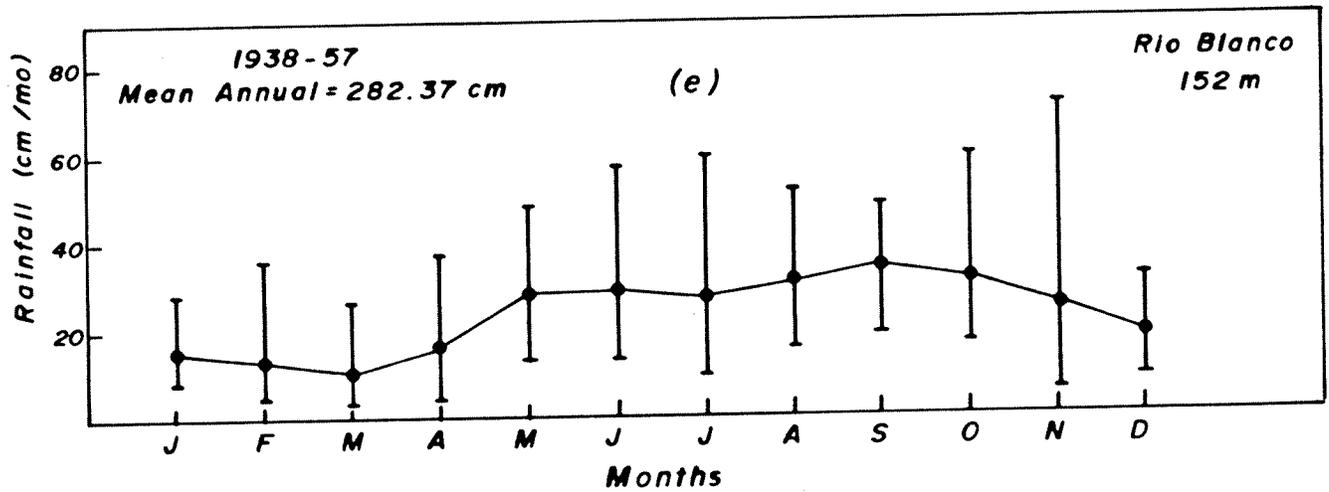
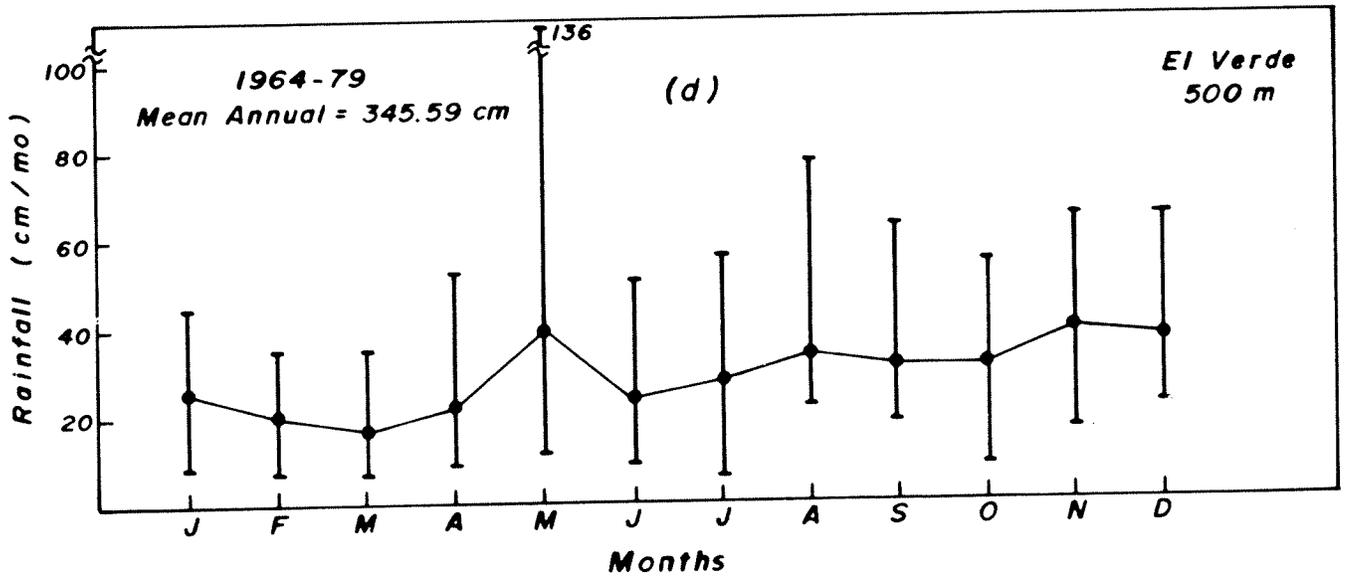


Figure 10.—Maximum, minimum, and mean monthly rainfall for stations in and adjacent to the Luquillo Experimental Forest (data from U.S. Department of Agriculture, 1909-1914, 1915-1921, 1921-1939; U.S. Department of Commerce, 1940-1952, 1955-1979).—Continued

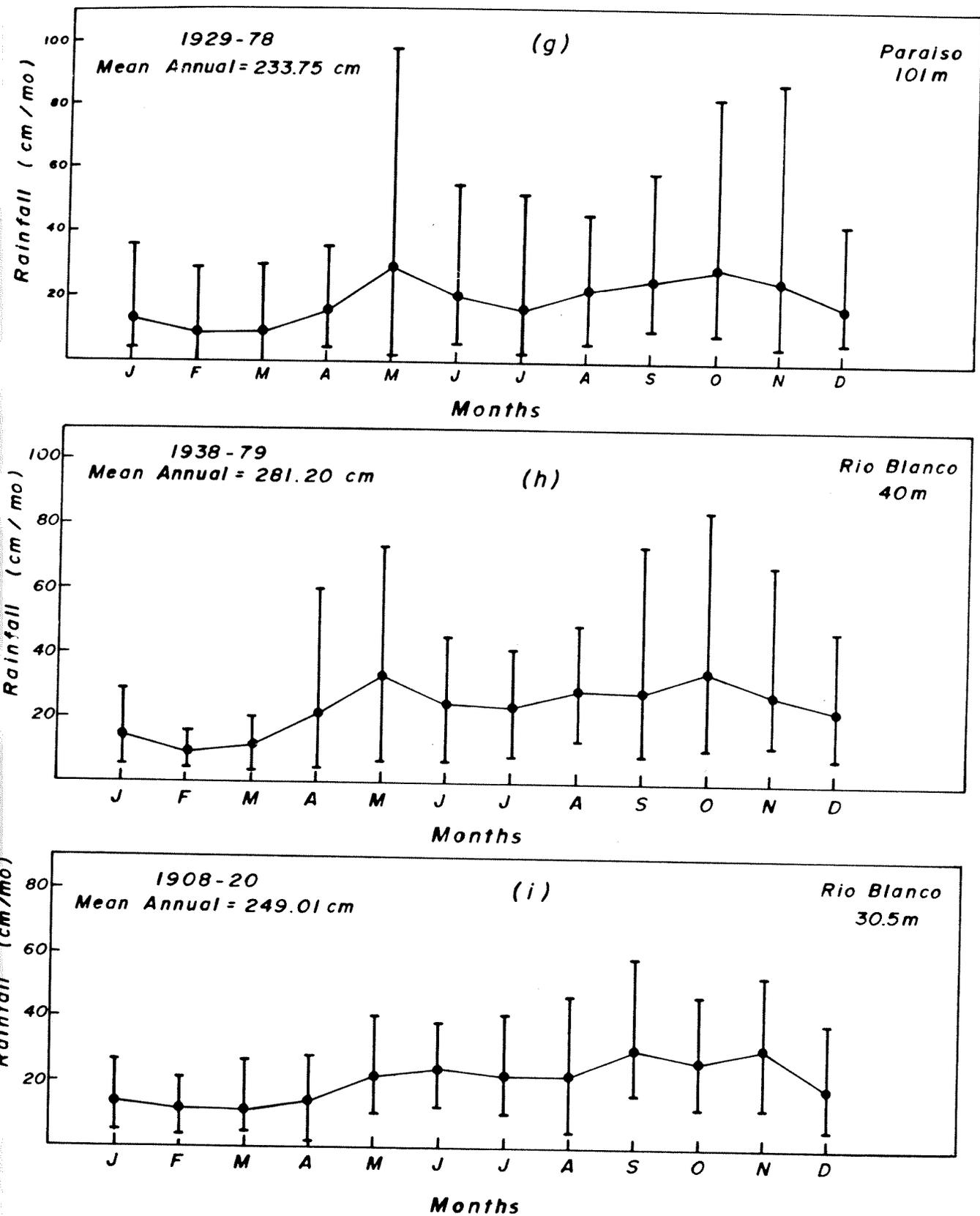


Figure 10.—Maximum, minimum, and mean monthly rainfall for stations in and adjacent to the Luquillo Experimental Forest (data from U.S. Department of Agriculture, 1909-1914, 1915-1921, 1921-1939; U.S. Department of Commerce, 1940-1952, 1955-1979).—Continued

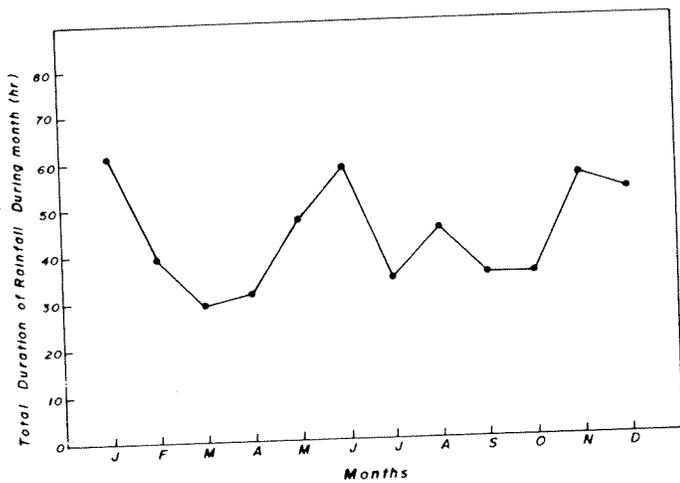


Figure 11.—Monthly duration of rainfall for the La Mina station (adapted from Wadsworth 1949).

Table 8.—Description of weather stations used in the study by Briscoe (1966)

El Yunque peak is one of the highest and the most conspicuous peaks in the Luquillo Mountains. The weather site was right at the peak proper, with the wind instruments and temperature tower extending above. Although approximately 19 km from the northeast corner of Puerto Rico, there is no major obstruction to the sweep of the winds, if anything, the shape of the topography tends to funnel prevailing winds directly toward the peak.

Cape San Juan is the most northeastern portion of Puerto Rico, 19 km northeast of El Yunque peak. The weather site was adjacent to the light station on a low hill, fully exposed to the northeast trade winds. Vegetation is sparse and desert-like.

Catalina nursery site was 4.8 km north of El Yunque, on a north slope. Weather instruments were situated among the nursery seedbeds.

Rio Blanco hydroelectric plant is 6.4 km south of El Yunque. The instruments were on a grassy area at the base of a very steep, high, wooded mountainside. Wind data from this station were strongly affected by local relief.

Cubuy was on an exposed shoulder. It was set in a forest, but with all trees removed within a radius equal to their own height above instrument level. Location is 11.2 km southwest of El Yunque.

Rio Grande was 4.8 km southwest of El Yunque; it was about halfway up a west-facing slope, as was Cubuy.

Sabana 8 was a little less than 8 km northeast of El Yunque, on a north-facing slope.

Sabana 4 was 4.8 km east of El Yunque, on an east-facing slope.

maximum annual variation. The annual variation in relative humidity at this station was about 12%, from a low of 63% to a high of 77%. The annual course of relative humidity was fairly constant for all other stations.

Diurnal variation in relative humidity at El Yunque was smaller than diurnal variation at lower elevation stations (fig. 19a and 19b). The difference between the minimum and maximum relative humidity at El Yunque was approximately 5%, whereas at the other stations the difference was 20–30%. Minimum relative humidity for all stations occurred between 1200 and 1400 hours during both January and June. The discontinuities that appear in these data for some stations appear to be errors in the original data.

Wind Velocity and Direction

Wind velocity was highest in any given month at the El Yunque station (8–18 km/hr) and gradually decreased towards the lowest elevation station at Río Blanco (1.5–3 km/hr, fig. 20). Peak wind velocities of approximately 16–18 km/hr at El Yunque occurred in January, April and September. Maximum wind velocity for the Catalina station (5–6 km/hr) occurred in April and July. The lowest elevation station (Río Blanco) exhibited a fairly constant wind velocity throughout the annual cycle. The average wind velocity at El Yunque was approximately six times higher than the wind velocity at Río Blanco.

The diurnal variation in wind velocity for the months of January and June are shown in figure 21a and b. Minimum wind velocity occurred at the highest elevation station (El Yunque) during the mid-day hours; however, maximum wind velocity occurred at this time at the lower elevation stations. The difference between the minimum and maximum wind velocity during the diurnal period decreased with increasing elevation. For example, the lowest elevation station had a 3.5 km/hr difference between the minimum and maximum velocity and the highest elevation station had a 1.5 km/hr difference.

Mean monthly wind direction for stations in and adjacent to the Luquillo Experimental Forest is given in figure 22. Wind direction is expressed on a numerical scale with 1 representing north-northeast, 4 representing due east, 8 representing due south, 12 representing due west, and 16 representing due north. The prevailing winds in this region of the globe are the Trades which blow out of the northeast.

At El Yunque northeast winds occurred from February to August, and again from October to December. January and September were the only two months at El Yunque when winds blew from the

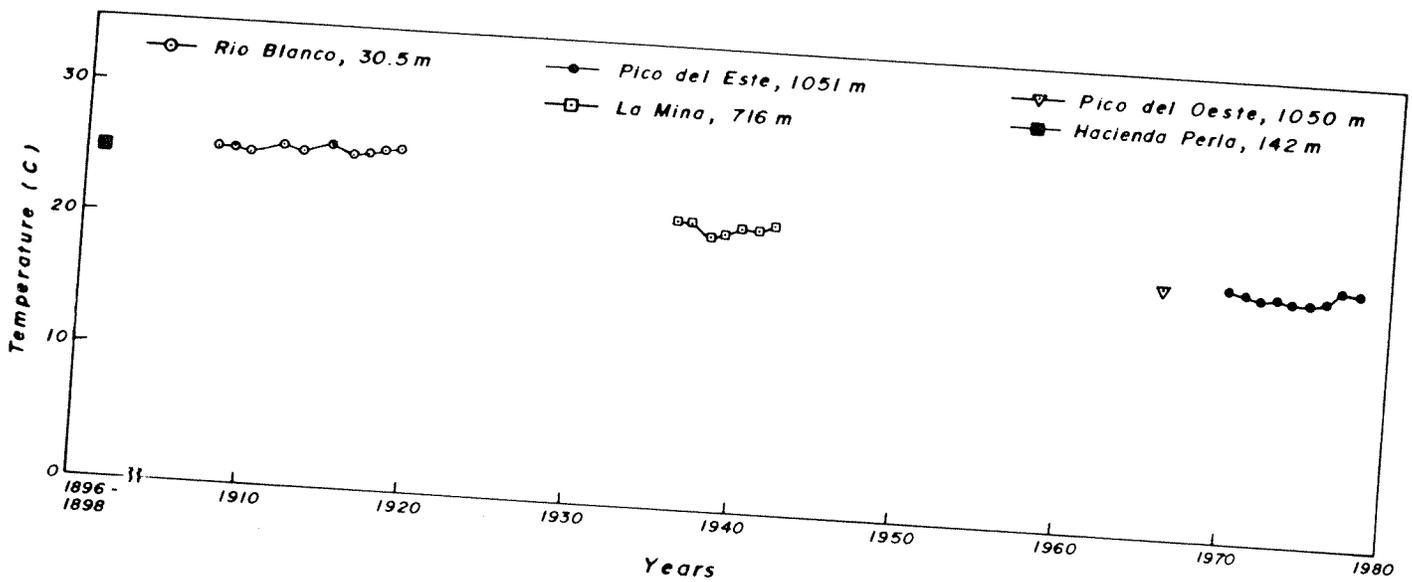


Figure 12.—Patterns of annual temperature for stations in and adjacent to the Luquillo Experimental Forest (data are from U.S. Department of Agriculture, 1909–1914, 1915–1921, 1921–1939; U.S. Department of Commerce, 1940–1952, 1955–1979; Wilson, 1899).

south. At low elevation stations winds blow from the south during a longer period.

During January, diurnal variation in wind direction was greatest for Río Blanco (fig. 23a). Between the hours of approximately 1000 and 1800 wind direction was approximately southwest at this station, but during the remainder of the day the wind blew from the southeast. Wind direction was fairly uniform throughout the day at the two higher elevation stations. A diurnal variation still occurred for Río Blanco in June, whereas little diurnal variation occurred at the other two stations (fig. 23b). In fact, at El Yunque, wind blew from a constant northeasterly direction.

Solar Radiation

The annual pattern of total incoming solar radiation for El Yunque and Cape San Juan at sea level was similar (fig. 24). However, the absolute amount of radiation measured at El Yunque (170–370 lg/day) was about half that measured at Cape San Juan (330–620 lg/day). Minimum solar radiation was measured in December at both stations, but total radiation at Cape San Juan was approximately twice that of El Yunque. Baynton (1968) also found minimum incoming radiation for the month of December at Pico del Oeste, a station similar in altitude to El Yunque. During the summer months radiation at Cape San Juan was also approximately twice that measured at El Yunque.

Maximum daily solar radiation measured at El Yunque during January (45 lg/hr) was similar to that measured in June (fig. 25a and b). A similar

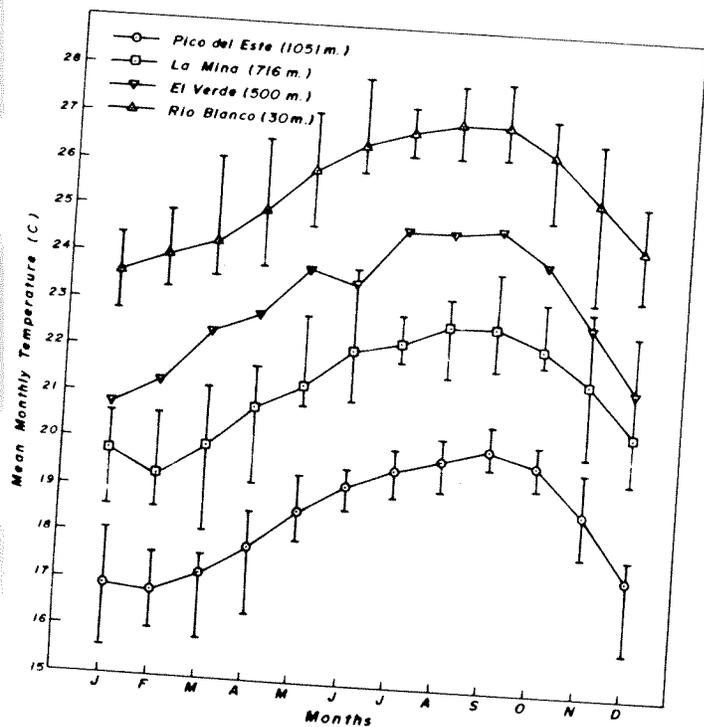


Figure 13.—Maximum, minimum, and mean monthly temperatures for stations in and adjacent to the Luquillo Experimental Forest (data are from U.S. Department of Agriculture, 1909–1914, 1915–1921, 1921–1939; U.S. Department of Commerce, 1940–1952, 1955–1979).

trend was measured at Cape San Juan for these two months; maximum daily solar radiation at this station was 67 lg/hr. Maximum radiation measured at Cape San Juan during either month was approximately 1.5 times higher than the maximum radiation measured at El Yunque during the corresponding month.

SURFACE HYDROLOGY

Six major rivers have their headwaters in the Luquillo Experimental Forest. The lengths of these rivers and the areas of their watersheds are given in table 9. Although the Río Espíritu Santo drains the largest area of the Luquillo Experimental Forest, the Río Grande de Loíza is the longest river. The Río Espíritu Santo, Río Grande de Loíza, Río Mameyes, and the Río Sabana flow in a northerly direction, and the Río Fajardo flows in an easterly direction, and the Río Blanco flows south (fig. 26).

Four streams within and adjacent to the Luquillo Experimental Forest have been monitored for water discharge since about 1968 (table 10). These stream gauges are located in two watersheds and at elevations ranging from 12–515 m (fig. 7). Mean annual discharge was directly related to elevation of the gauging station (table 10). Variation in the annual discharge, as measured by the coefficient of variation, was lowest for the highest and lowest elevation stations.

The pattern of annual water discharge of streams in the Luquillo Experimental Forest was similar for all stations; only the magnitudes are different (fig. 27). For most streams the two consecutive years of 1969 and 1970 had unusually high flows. The rainfall in 1970 was the highest on record since 1931 (c.f. fig. 8)

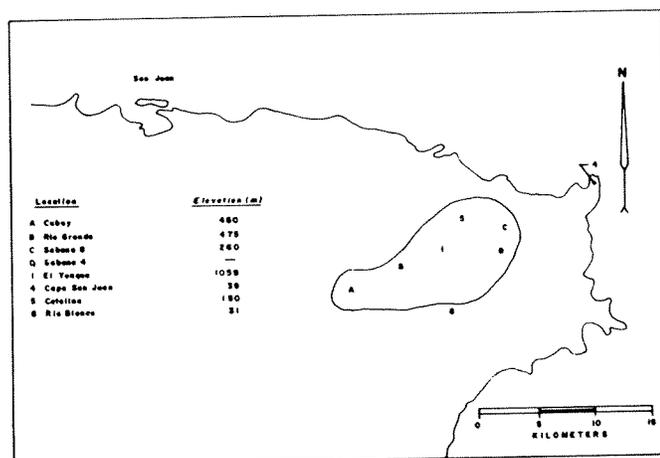


Figure 14.—Location of weather stations in and adjacent to the Luquillo Experimental Forest used in the study by Briscoe (1966). Descriptions of each station are given in table 8.

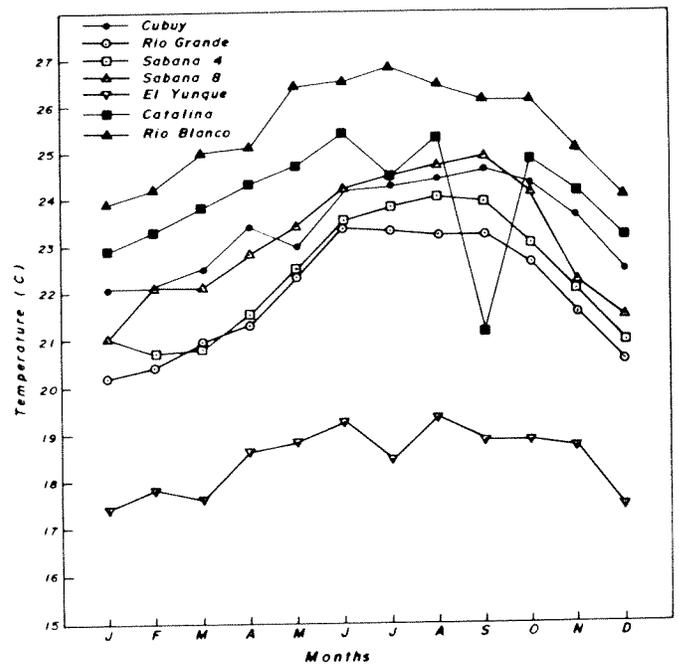


Figure 15.—Mean monthly temperature for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

due to a slow moving tropical depression and a series of slow moving cold fronts.

The pattern of mean monthly stream discharge was generally the same for all the stations monitored in the Luquillo Experimental Forest (fig. 28a–d). The magnitudes, however, generally decreased from high to low elevation stations. Mean monthly stream discharge peaked in May and again in October–December. Monthly stream discharge pattern generally tracked monthly rainfall (fig. 28a). Monthly stream discharge was more variable for the high elevation station than for the lower ones, although the latter were more variable on a yearly basis (table 10). For example, the range of water discharges from the high elevation station was wider than for the low elevation station (c.f. fig. 28a and 28c–d). Most variability in discharge was recorded during the months when peak discharge occurred.

Because stream discharge and rainfall data were collected at different stations and over different time periods, relationships between discharge and rainfall cannot be made. However, a comparison of the discharge data (table 10) with the rainfall (table 6) does suggest that discharge accounts for a high proportion of the rainfall.

In 1964, Bogart et al. conducted a study on a small watershed (elevation 600 m) of the Río Hiaco in the Luquillo Mountains. The results of this study showed that 85% of rainfall was discharged by streams. At lower elevations in the Luquillo Experimental For-

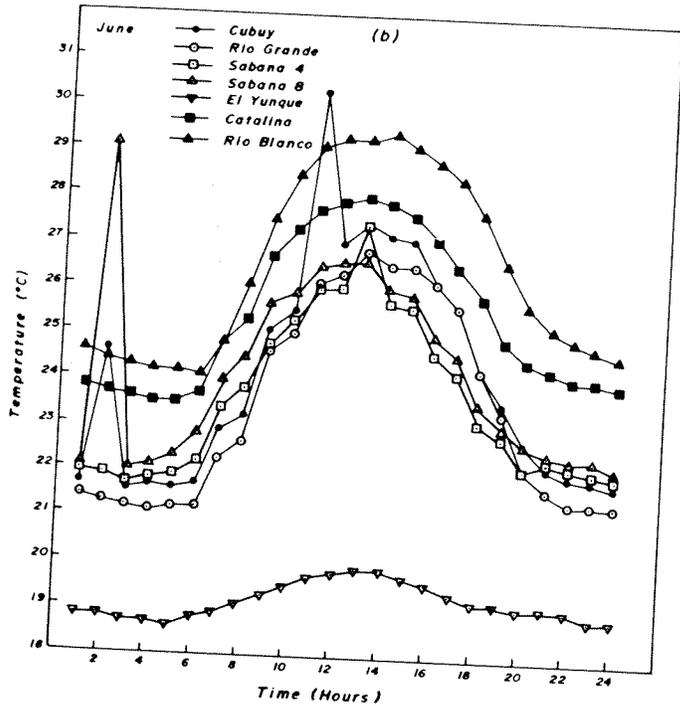
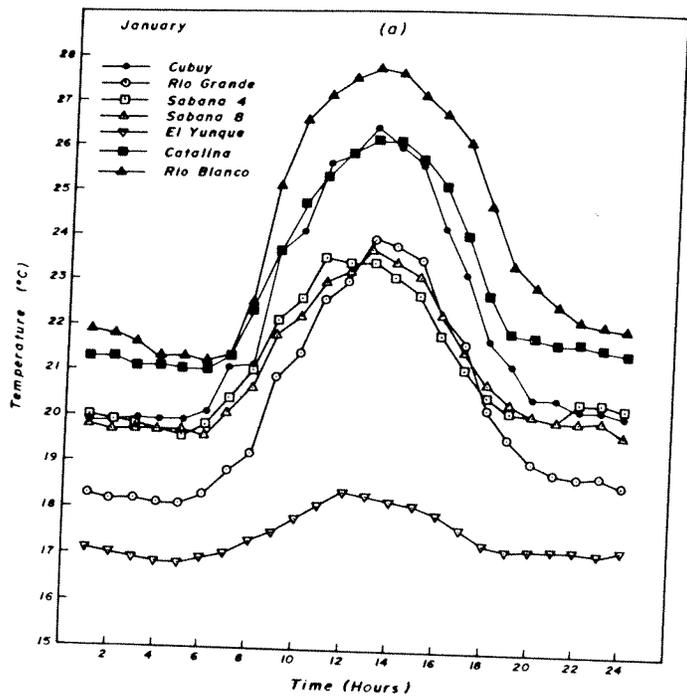


Figure 16.—Diurnal variation in temperature for the month of (a) January and (b) June for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

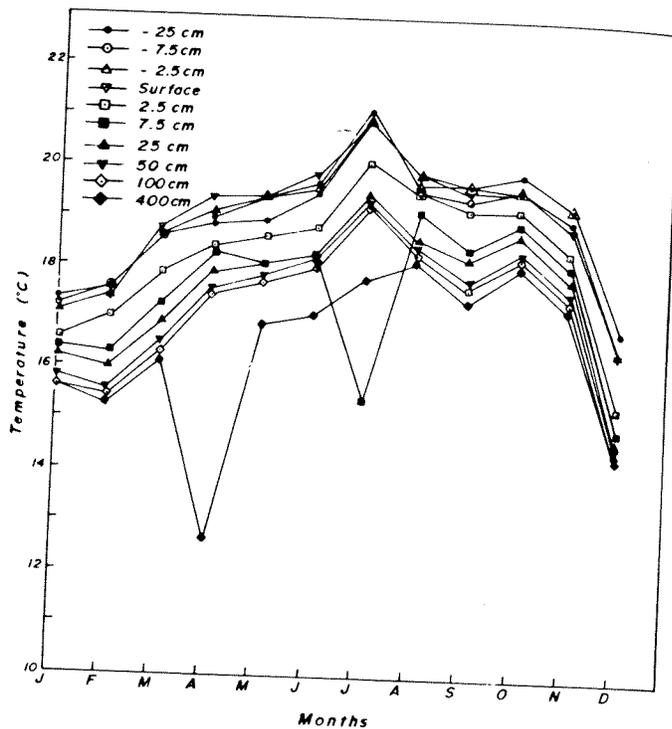


Figure 17.—Temperature profile from 25 cm below to 400 cm above soil surface at El Yunque. (data are from Briscoe 1966).

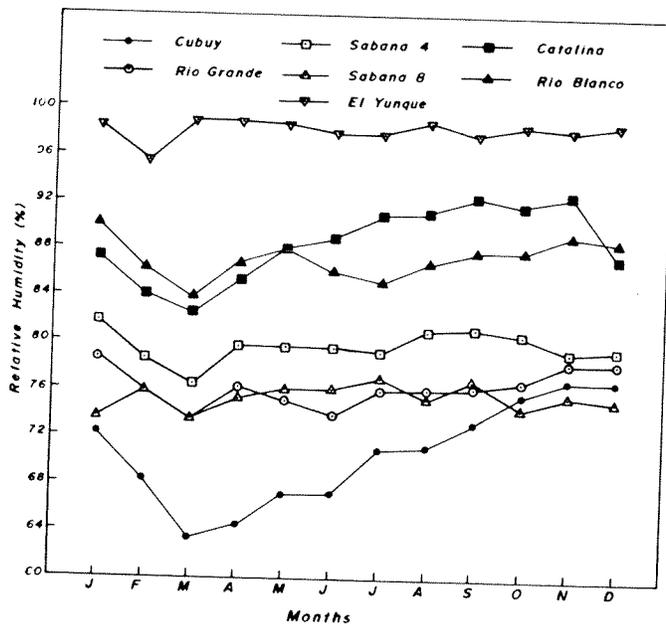


Figure 18.—Mean monthly relative humidity for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

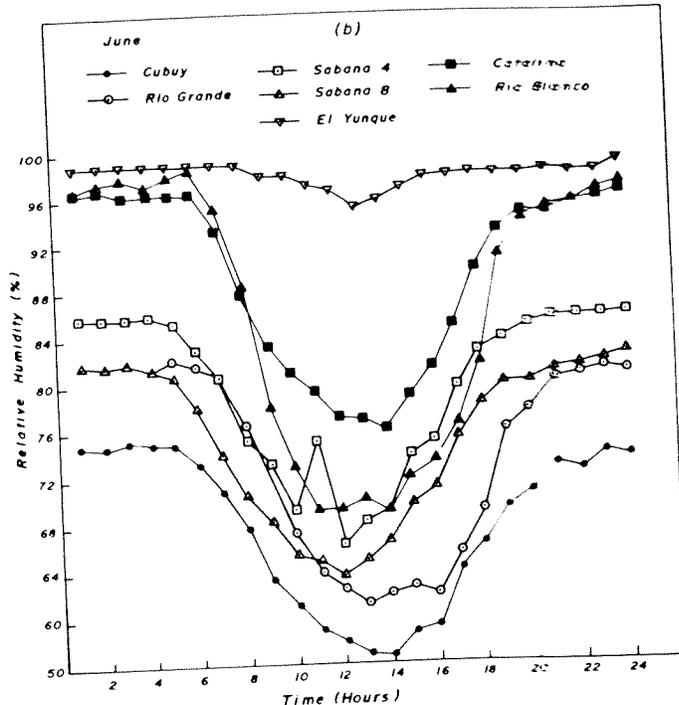
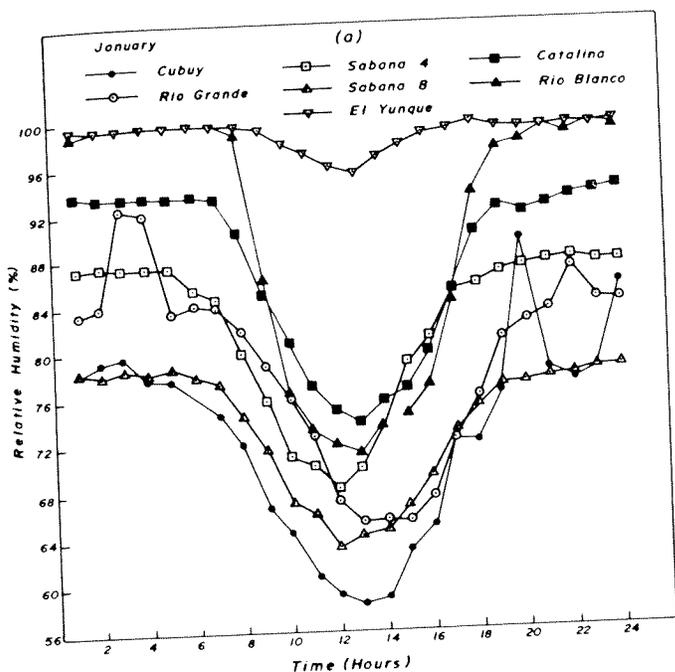


Figure 19.—Diurnal course of relative humidity for the months of (a) January and (b) June for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

est (El Verde site) 52% of rainfall was discharged by streams (Odum et al. 1970), whereas at higher elevations (approximately 1,000 m) Baynton (1968 and 1969) found that 95% of rainfall was discharged by streams. All these results suggest that at high elevations, where the forest is generally shrouded in clouds, either evapotranspiration (the difference between rainfall and runoff) is extremely low, inputs of water from condensation are a significant component of the water budget, or a combination of these two phenomena are occurring. At lower elevations, where the forest is rarely shrouded in clouds, evapotranspiration from the forest becomes a significant component of the water budget.

WATER QUALITY OF RIVERS

Riverine waters of the Luquillo Experimental Forest are cool, neutral to slightly basic, low in conductivity, and generally oligotrophic (table 11). Water quality parameters generally increased in value along a gradient from high to low elevations for the three stations in the Luquillo Experimental Forest (the two Río Espiritu Santo stations and the Río Mameyes station). The Río Grande station was located outside the boundaries of the Forest and the river at this point was probably influenced by human activity, resulting in higher values for many of the water quality parameters.

Table 9.—Watershed areas and lengths of rivers in the Luquillo Mountains (adapted from Wadsworth 1949)

River	Estimated total length (km)	Estimated watershed area within forest land (ha)
Espiritu Santo	12	4,977
Grande de Loiza	59	4,753
Blanco	16	3,791
Mameyes	18	2,465
Fajardo	18	2,053
Sabana	10	1,609
Total		19,648

The physical and chemical parameters of the Espiritu Santo Drainage Basin were measured for approximately 6 months along a gradient from headwaters to the mouth of the Río Espiritu Santo (Cuevas and Clements 1975). Of the nine stations sampled, five were located in or very near to the boundary of the Luquillo Experimental Forest. Results of the water quality parameters for eight of these stations (excluding the mouth of the river) are shown in figures 29 and 30. With the exception of chloride, the concentration of oxygen, carbon dioxide, four major cations, and temperature remained constant throughout a six-month period extending from October to April 19. However, the concentration of calcium and chloride measured by Cuevas and

Clements (fig. 30) are considerably different from those given in table 11; calcium was lower and chloride was higher in figure 30 than in table 11. The samples in table 11 were collected over several years, while those in figure 30 were collected over six months.

Chloride concentration varied considerably during the sampling period, perhaps due to changes in wind direction. Winds from the ocean may transport salt spray to high altitudes (Odum 1970a).

The export of total dissolved solids by rivers of the Luquillo Experimental Forest is linearly related to discharge of the rivers (fig. 31a-c). The average annual export of total dissolved solids from streams for which we have records was estimated using the average annual discharge (table 10), the area of the watersheds, and the linear regressions in figure 31a-c. The results are: 953 t/yr and 2,320 t/yr for Río Espiritu Santo stations 633 and 638, respectively, and 3,324 t/yr for Río Mameyes station. Although stream discharge was 1.5-2 times higher at the upper station (No. 633) than at the two lower elevation stations (No. 638 and Mameyes), export of total dissolved solids from the upper R. Espiritu Santo was 2.4-3.5 times lower than Export from the lower elevation stations.

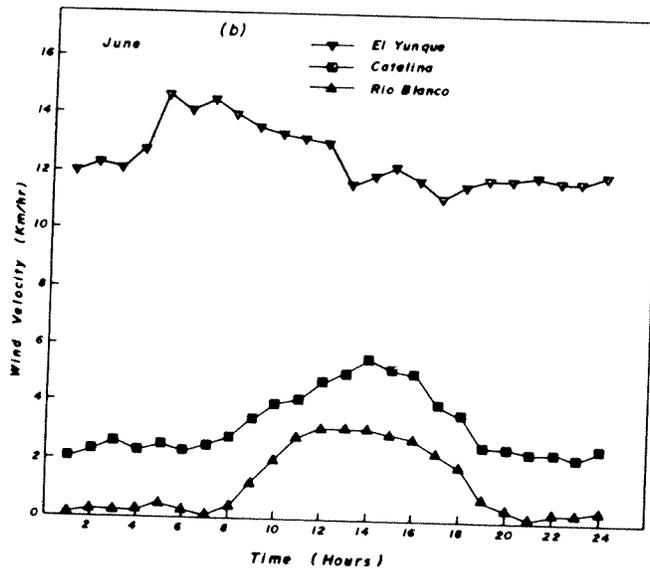
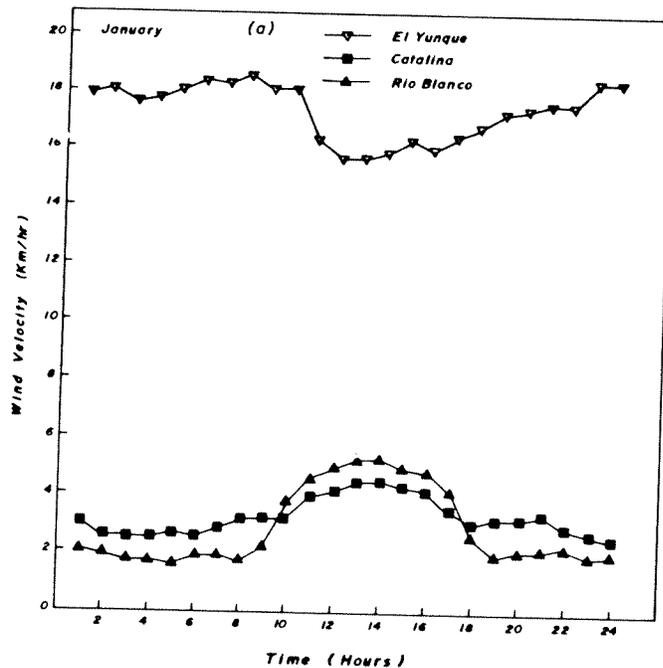


Figure 21.—Diurnal variation in wind velocity for (a) January and (b) June for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

GEOLOGY

The geology of the Luquillo Experimental Forest area has been mapped and described by Seiders (1971). He described the Forest area as a completely faulted and folded terrain. It is underlain by Cretaceous volcanic rocks and subordinate Cretaceous and/or Tertiary intrusive bodies and minor lower Tertiary volcanic and sedimentary rocks. Andesitic igneous rocks which contain some interbedded ma-

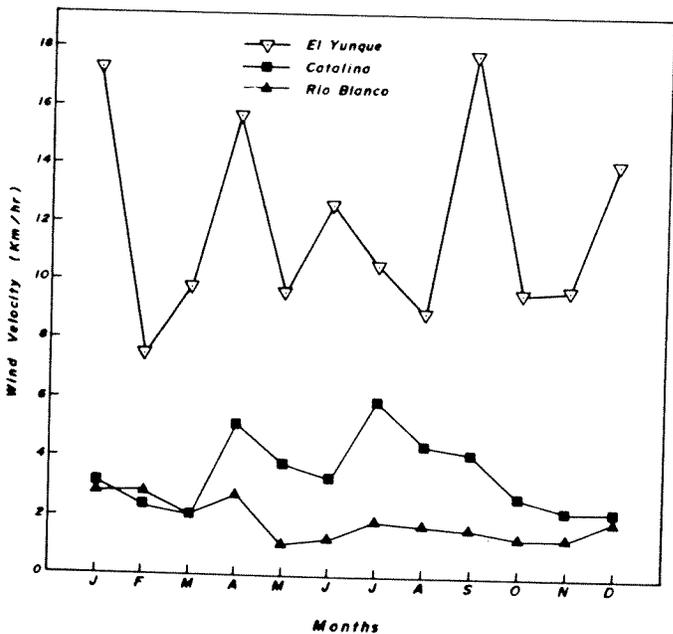


Figure 20.—Mean monthly wind velocity for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

rine deposited mudstones cover most of the area of the Forest. Quartz diorite and diorite intrusions are exposed in the southeastern part of the Forest, and diorite dikes are located in the west central part. Some alluvial deposits of sand, gravel, silt and clay are found in the floodplains of streams with similar deposits (terrace deposits) found slightly above the present flood level.

SOILS

Surveys and Series Documentation

Soils in the Luquillo Experimental Forest were first mapped by Roberts (1942) at a scale of 1:50000. A modern survey of eastern Puerto Rico, including the Luquillo Experimental Forest, was published by the USDA Soil Conservation Service (SCS) (Boccheciamp 1977). The scale for the field mapping units was 1:20000. There are four soil associations within the Luquillo Experimental Forest (table 12) representing 19 soil series. Using classification terminology from the Soil Taxonomy system (USDA Soil Conservation Service 1975), the principal soil orders are Ultisols and Inceptisols which occupy approximately 50 and 20%, respectively, of the Luquillo Experimental Forest (table 13; fig. 32).

Los Guineos is the most extensive series in the Luquillo Experimental Forest. It and the Humatas series are quite typical of upland Ultisols. They are deep, highly weathered and leached, with low pH values, and base saturations less than 35% at 1.25 m (Beinroth 1971). In general the Ultisols include most soils that have been called Reddish-Brown Laterites, Red-Yellow Podzolics, and even Ground-Water Laterites. Though of limited extent in the Luquillo Experimental Forest, the Múcara series is one of the most extensive soils in Puerto Rico (Miranda-Siragusa 1967). This representative Inceptisol is characterized by less weathering and no significant illuviation or leaching. Profile descriptions and laboratory data for typical Los Guineos and Múcara profiles are given in tables 14 and 15.

Locally, there are smaller soil field units that could not be mapped separately at the 1:20000 scale. One of these inclusions, Catalina clay, is classified as a Tropic Haplorthox, and belongs to the Oxisol soil Order (USDA Soil Conservation Service 1969; Lugo-López and Rivera 1977). Oxisols, considered the oldest and most weathered soils in the Soil Taxonomy classification scheme, produce important agricultural crops in Puerto Rico (Beinroth 1971).

In both the Roberts and recent SCS surveys, large areas within the Luquillo Experimental Forest were

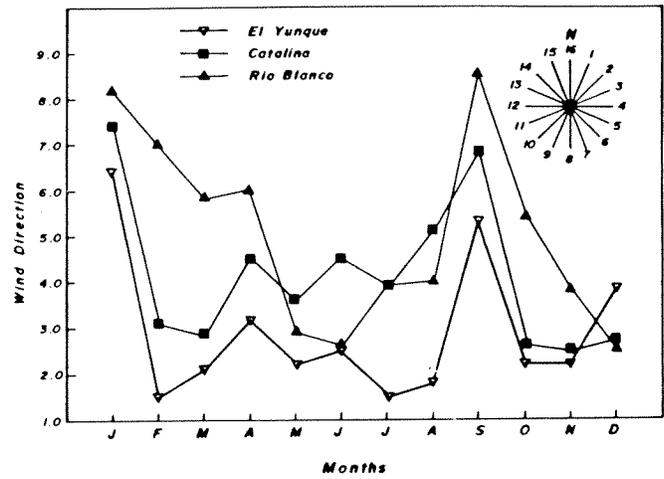


Figure 22.—Mean monthly wind direction for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

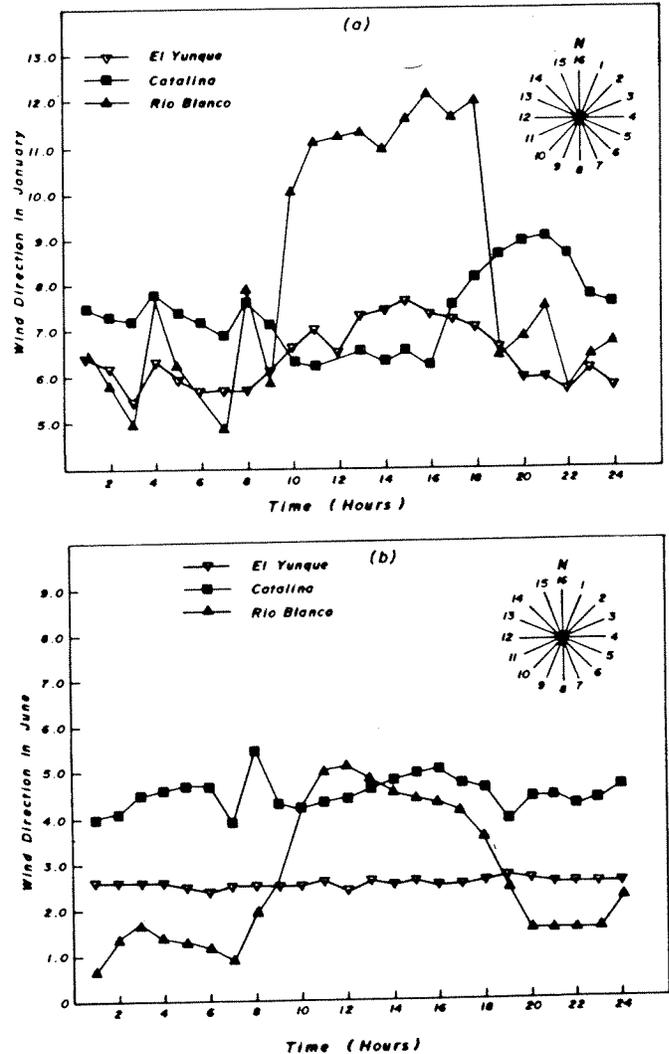


Figure 23.—Diurnal variation in wind direction for (a) January and (b) June for stations in and adjacent to the Luquillo Experimental Forest (data are from Briscoe 1966).

Table 10.—Station description and mean annual discharge for stream gauging stations within and adjacent to the Luquillo Experimental Forest

Station	I.D. ^a no.	Elevation (m)	Lat. °N	Long °W	Period of record (yr)	Mean annual discharge (cm)	S.E. ^b	C.V. ^c (%)
Rio Espiritu Santo Basin								
Rio Espiritu Santo near El Verde	633	515	18°19'	65°49'	6	469	45	23
Rio Grande near El Verde	642	38	18°21'	65°50'	8	268	42	45
Rio Espiritu Santo near Rio Grande	638	12	18°22'	65°49'	10	214	20	29
Rio Mameyes Basin								
Rio Mameyes near Sabana	655	84	18°20'	65°45'	6	300	44	36

^aU.S. Geological Survey identification.

^bStandard error of the mean.

^cCoefficient of variation (C.V.) = (standard deviation/mean) × 100.

Table 11.—Mean water quality parameters of rivers draining the Luquillo Experimental Forest. Data are for the period 1969–1974 (U.S. Department of Interior, Geological Survey, 1968–1977). One standard error is given in parenthesis

Parameter	Río Espiritu Santo (515 m) ^a (n=31)	Río Mameyes, Sabana (84 m) ^a (n=34)	Río Grande El Verde (38 m) ^a (n=12)	Río Espiritu Santo (12 m) ^a (n=15)
Temperature (C)	21.4 (0.5)	22.9 (0.2)	24.8 (0.7)	24.7 (0.7)
Specific conductance (mmhos)	56.6 (2.9)	85.3 (17.1)	107.9 (6.5)	184.9 (95.2)
pH	6.9 (0.09)	7.2 (0.10)	7.5 (0.10)	7.1 (0.11)
Alkalinity (mg/l)	14.1 (1.7)	32.8 (2.7)	39.5 (3.2)	23.7 (6.5)
Ca (mg/l)	3.9 (0.3)	10.5 (0.4)	8.6 (0.7)	6.6 (0.8)
Mg (mg/l)	1.7 (0.1)	2.5 (0.03)	4.2 (0.3)	3.0 (0.5)
Na (mg/l)	5.6 (0.1)	6.7 (0.2)	8.5 (0.4)	6.8 (0.4)
K (mg/l)	0.42 (0.05)	0.60 (0.04)	0.43 (0.02)	0.40 (0.02)
Cl (mg/l)	7.7 (0.1)	8.4 (0.2)	10.3 (0.4)	9.1 (0.6)
SO ₄ (mg/l)	2.2 (0.2)	4.0 (0.4)	2.5 (0.3)	2.6 (0.3)
NO ₃ (mg/l)	0.23 (0.07)	0.20 (0.05)	0.10 (0.03)	0.01 (0.01)
Dissolved PO ₄ (mg/l)	0.05 (0.03)	0.30 (0.3)	0.04 (0.04)	0.03 (0.02)

^aelevation.

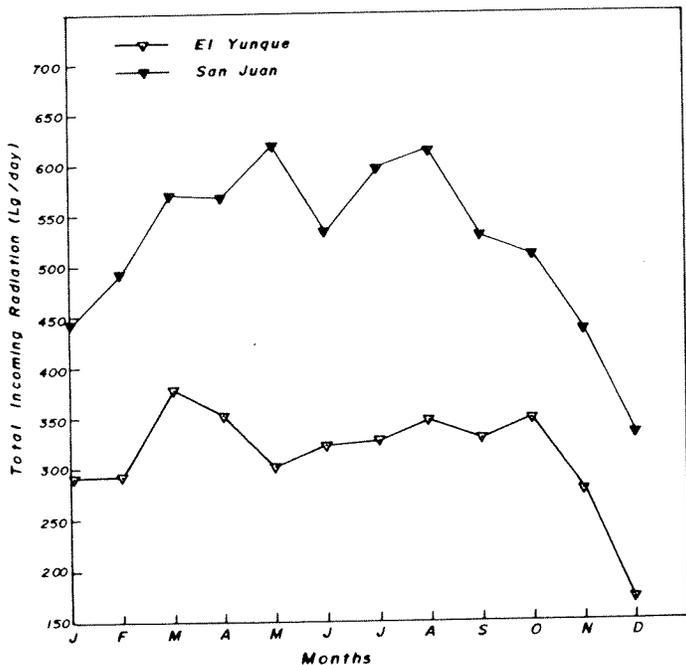


Figure 24.—Total incoming solar radiation for El Yunque in the Luquillo Experimental Forest and for Cape San Juan in the northeastern point of Puerto Rico (data are from Briscoe 1966).

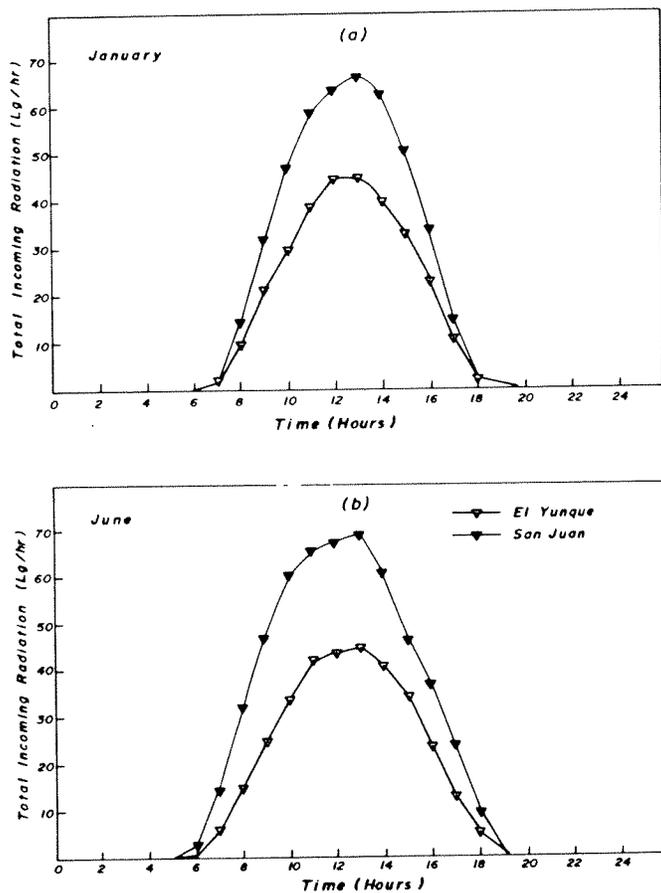


Figure 25.—Diurnal variation in incoming radiation for (a) January and (b) June for El Yunque and Cape San Juan (data are from Briscoe 1966).

Table 12.—Major soil associations within the Luquillo Experimental Forest (adapted from Boccheciamp 1977)

Association	Characteristics
Caguabo-Múcara-Naranjito	Shallow and moderately deep, well-drained, sloping to very steep soils on volcanic uplands.
Coloso-Toa-Bajura	Deep, moderately well-drained to poorly drained, nearly level soils on flood plains.
Los Guineos-Guayabota-Rock land	Shallow to deep, well-drained to poorly drained, strongly sloping to very steep soils on volcanic uplands of tropical rain forest.
Los Guineos-Humatas-Lirios	Deep, well-drained and moderately well drained, gently sloping to very steep, acid soils on volcanic uplands.

mapped as rough stony land (fig. 32). These areas usually occur on high, jagged mountain peaks and on long, very steep side slopes where rocks and boulders cover 75 to 90% of the surface. To meet the needs for greater development of the Forest for recreational, watershed, timber, and other uses, National Forest staff initiated more detailed soil surveys within the Forest in 1978.

In summary, soils within the Luquillo Experimental Forest are quite diverse taxonomically. They include major series, capable of supporting various forest types and agricultural crops, which are found extensively throughout the rest of the island. They represent three major soil Orders and possibly four if little-studied inclusions are incorporated. Relatively large-scale and recent soil surveys exist for the Forest that can be used for most future planning and development projects.

Physical Properties

Soil profile data are mainly available from recent surveys and laboratory investigations of the SCS in Puerto Rico (1967, 1969; Carter 1965; Boccheciamp 1977). Typical information for each horizon includes depth, structure and consistency, mottling extent, and soil color. Other soil profile data are available from Lyford (1969), describing a soil under dwarf (elfin) forest in the Luquillo Experimental Forest, and from Odum (1970a), presenting data for three sites at El Verde using SCS terminology.

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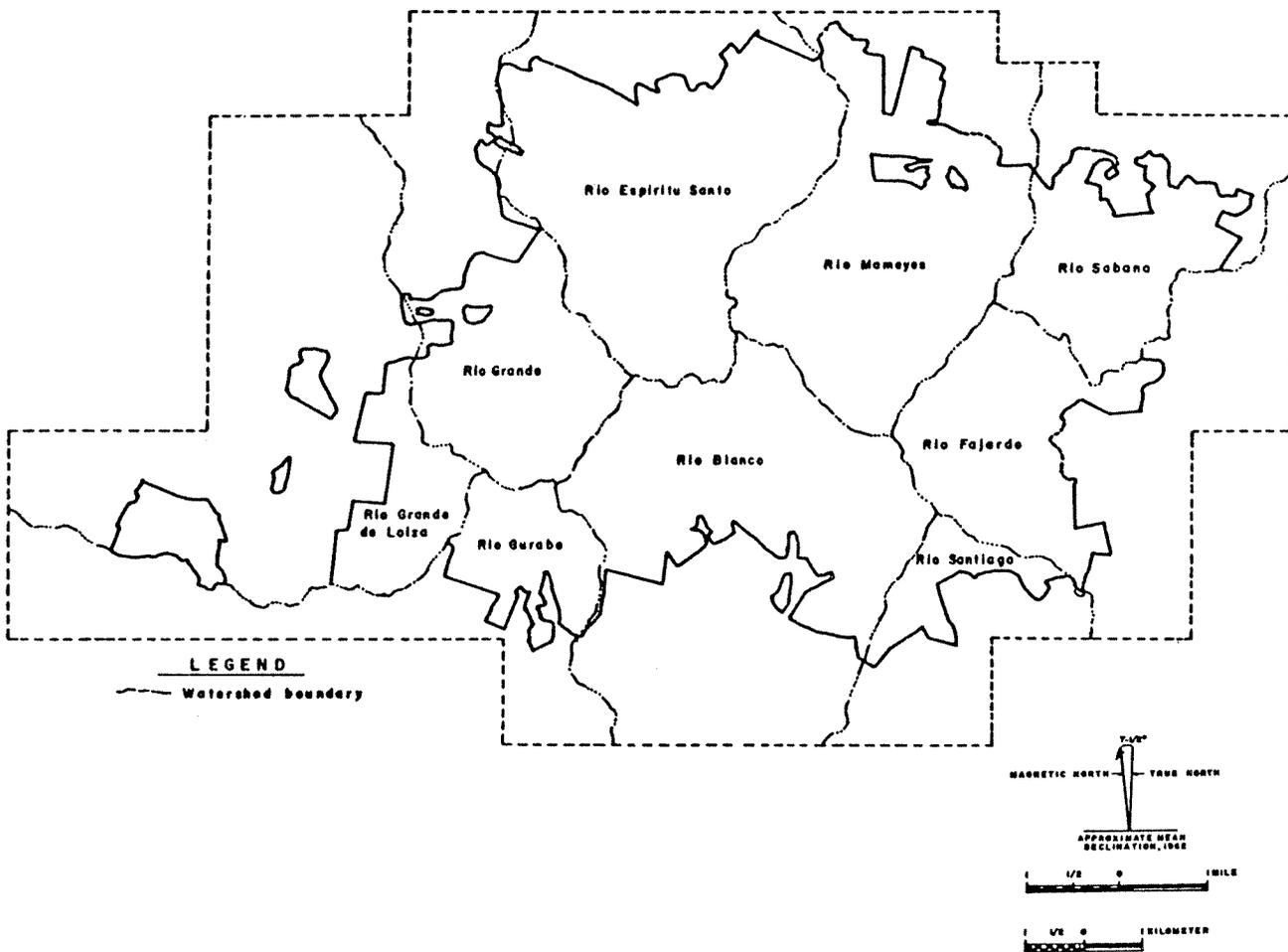


Figure 26.—Location of watersheds in the Luquillo Experimental Forest.

After analyzing soil structure, moisture, and density and structure of the forest vegetation in the Forest, the U.S. Army Corps of Engineers (1960) found: 1) the average year-long rate of daily soil moisture loss in the surface to 30 cm layer was about one-half that of the average U.S. summer rate and 2) soil moisture depletion rates did not vary with season and were relatively low as compared to those in temperate zones. The lower rates appeared to result from accumulated environmental effects like high and frequent rainfall, microclimatic “vapor blankets”, shorter summer days, lower maximum summer temperatures, and greater interception of short-wave length rays by high amounts of water vapor in the atmosphere.

Soriano-Ressy et al. (1970) did mechanical analyses of soils at two sites by wet sieving. They found that samples from 0–65 cm had a higher percentage of clays and fine materials, with 95% of their soils passing a no. 200 sieve; only 49% of other soils collected at 25–40 cm depths from Dominica passed the same sieve. Work by Weaver and Jagels (cited in Odum, 1970a) showed that soils from five stations

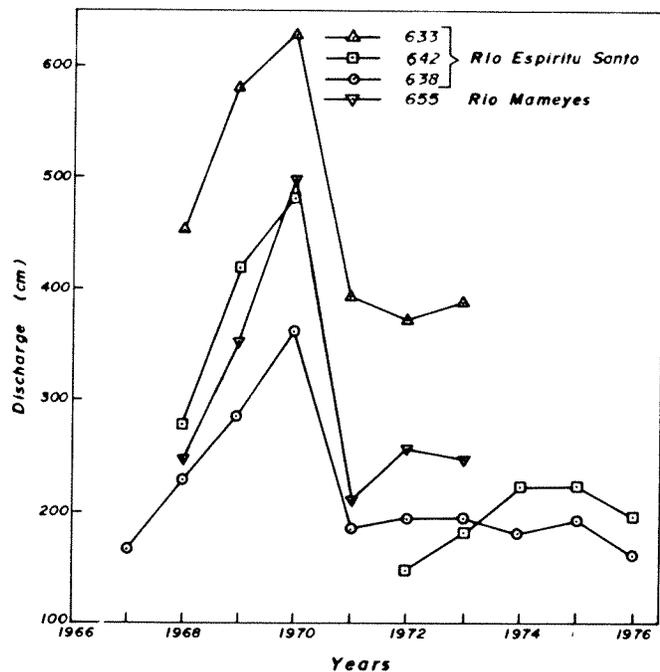


Figure 27.—Annual stream discharge for rivers draining the Luquillo Experimental Forest (data are from U.S. Department of Interior, 1967, 1968–1979).

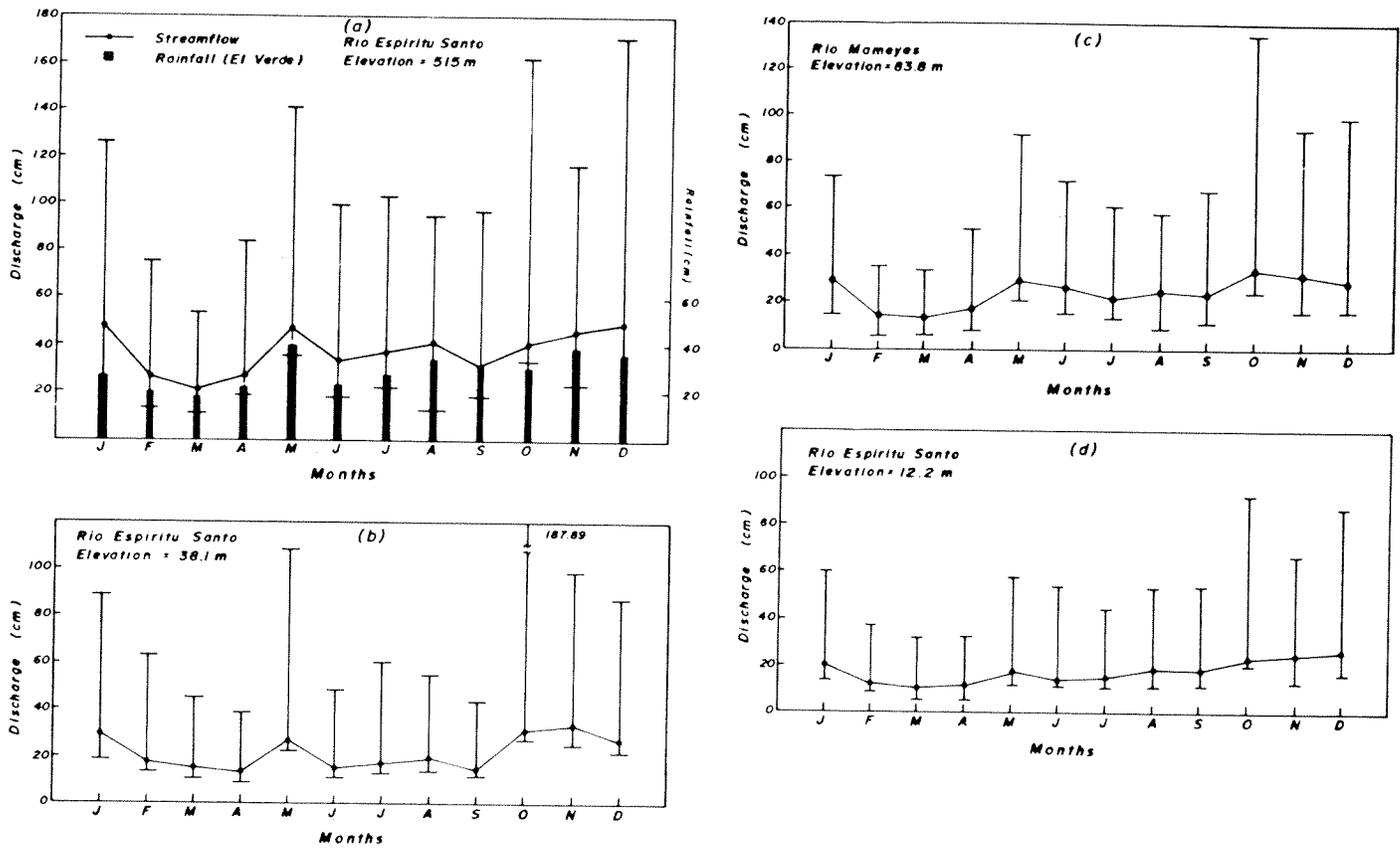


Figure 28.—Mean and range of monthly discharge from rivers draining the Luquillo Experimental Forest (data are from U.S. Department of Interior, 1967, 1968–1979).

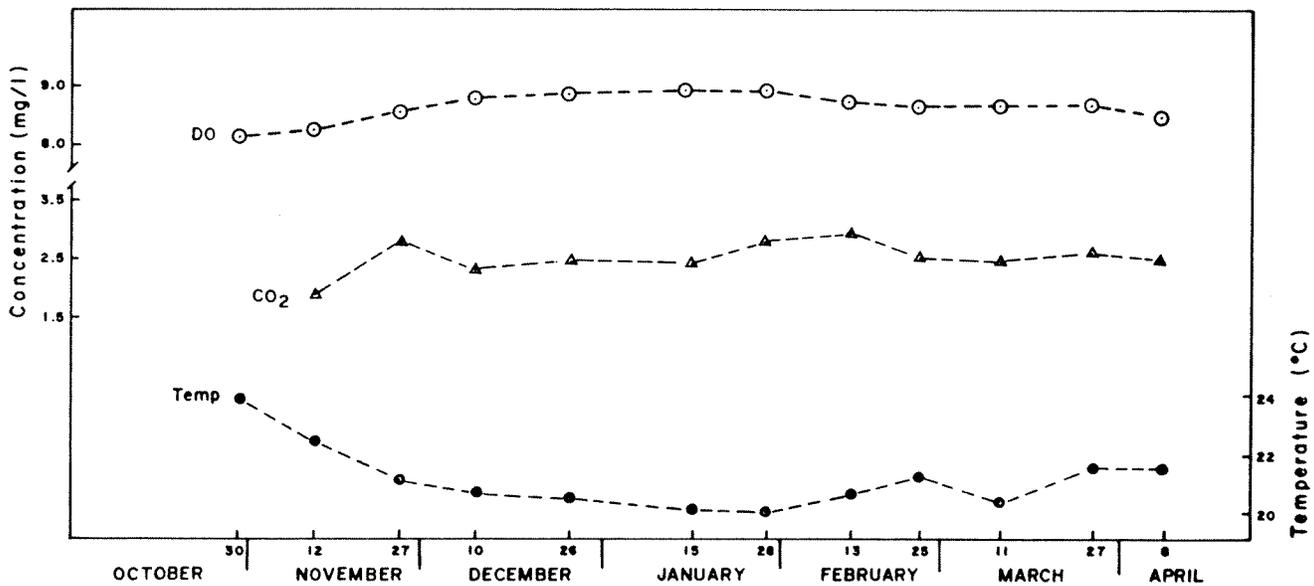


Figure 29.—Mean concentrations of dissolved oxygen (DO), free carbon dioxide (CO₂), and temperature (Temp) across time for stations on the Rio Espiritu Santo (Cuevas and Clements 1975).

Table 13.—Principal soil series located within the Luquillo Experimental Forest and some of their associated features

Soil Order ^a	Series	Classification ^a	Features
Ultisol	Los Guineos silty clay loam	Epiaquic Tropohumult	Deep, well-drained, strongly acid soils; slopes of 12–60%; parent material is fine textured residuum derived from highly weathered volcanic rock; very susceptible to erosion and difficult to work for agriculture; average annual precipitation is up to 2,540 mm.
Ultisol	Yunque silty clay loam	Epiaquic Palehumult	Deep, well-drained, strongly acid soils; slopes of 10–35%; parent material is fine textured residuum of volcanic rocks; high available water capacity and medium fertility; average annual precipitation is up to 4,700 mm.
Ultisol	Ciales silty clay loam	Aquic Tropohumult	Deep, strongly acid soils, poorly drained in upper part but well-drained in lower part; slopes of 12–45%; parent material is highly weathered residuum of igneous rocks; moderate available water capacity and medium fertility; average annual precipitation is up to 4,700 mm.
Ultisol	Picacho silty clay loam	Aquic Tropohumult	Deep, strongly acid, moderately well-drained soils; slopes of 20–50%; parent material is residuum from igneous rocks; moderate available water capacity and medium fertility; average annual precipitation is up to 4,700 mm.
Ultisol	Humatas clay	Typic Tropohumult	Deep, well-drained, very acid soils; slopes of 20–60%; parent material is residuum of basic volcanic rocks; high available water capacity and medium natural fertility; average annual precipitation is up to 2,200 mm.
Inceptisol	Guayabota silty clay loam	Lithic Trophaquept	Shallow, strongly acid, slowly permeable soils; slopes of 20–60% or more; parent material is residuum from dark bluish-grey siltstone; high available water capacity; average annual precipitation is up to 4,700 mm.
Inceptisol	Utulado clay loam	Typic Humitropept	Deep, strongly acid, well-drained soils; slopes of 40–100%; parent material is residuum of igneous rocks; moderate to low available water capacity; average annual precipitation is up to 4,700 mm.
Inceptisol	Múcara silty clay loam	Vertic Eutropept	Moderately deep, medium acid soils; slopes of 12–40%; parent material is residuum from basic volcanic rocks; high available water capacity and high fertility; average annual precipitation is 1,900–2,030 mm.

^aAdapted from U.S. Department of Agriculture 1967.

around El Verde also had high clay contents, ranging from 42.6 to 65.6% (table 16).

Bulk density data are more variable. Weaver and Jagels (cited in Odum 1970a) reported values of 0.71 to 0.87 g/cc. Edmisten (1970d) found that El Verde values varied from 0.66 to 1.18 (table 17). Jordan (1970a) found that the bulk density of a surface sample from 0 to 5 cm depth was 0.75, which was much lower than the 0.99 value for a below ground sample from 40 to 45 cm depth.

Water availability and movement is also quite variable depending on season, local topography, and soil series studied. For some series like Catalina clay, even with high clay contents, mean infiltration rates can surpass 22 cm/h (Bonnet and Lugo-López 1952; Lugo-López et al. 1968). On Pico del Oeste, at a dwarf forest site, Howard (1970) observed complete saturation and little soil water movement. He surmised that aeration could be a major factor in controlling root development and stunted nature

Table 14.—Selected profile and laboratory data for Los Guineos silty clay loam (clayey, mixed, isothermic Epiaquic Tropohumult)^a

Horizon	Depth (cm)	Profile data									
		Texture		Organic carbon (%)	Nitrogen (%)	Water content 15– Bar (%)	pH (1:1 in H ₂ O)				
Sand (2–0.05)	Silt (0.05–0.002) (%)	Clay (<0.002)									
Ap	0–13	Brown (10YF 4/3) clay loam with common fine distinct yellowish brown mottles; weak fine granular structure.									
B21t	13–38	Yellowish brown (10YR 5/6) clay with few fine distinct yellowish red (5YR 5/8) mottles; moderate course subangular blocky structure.									
B22t	38–61	Reddish yellow (7.5YR 6/8) clay; moderate course subangular blocky structure.									
B31t	61–86	Red (2.5YR 4/6) and strong brown (7.5YR 5/8) clay; weak fine and medium subangular blocky structure.									
B32t	86–122	Red (2.5YR 4/6) and reddish yellow (7.5YR 6/6) clay; weak fine and medium subangular blocky structure.									
		Extractable bases					Cations exchange capacity		Base saturation		
		Ca	Mg	Na	K	Sum	Sum cations	NH ₄ OAc	KCl Extractable Al	Sum cations	NH ₄ OAc
		----- (meq/100 g) -----					----- percent -----				
Ap	0–13	2.0	2.6	0.2	0.6	5.4	24.1	15.7	3.0	22	34
B21t	13–38	0.1	2.2	0.1	0.1	2.5	18.2	12.3	5.9	14	20
B22t	38–61	0.9	0.1	0.1	1.1	20.3	14.6	8.0	5	8
B31t	61–86	0.2	1.0	0.1	0.1	1.4	24.3	15.3	10.2	6	9
B32t	86–122	0.8	0.1	0.1	1.0	23.6	16.1	10.4	4	6

^aAdapted from U.S. Department of Agriculture, 1967.

of the dwarf forest. However, at some times of the year, water percolation at dwarf forest sites is quite rapid (Leon H. Liegel, Institute of Tropical Forestry, personal observation in March, 1979). Edmisten (1970d) measured better infiltration rates on slopes than on level areas; higher rates were usually associated with low bulk densities (table 18). Jordan (1970a) found that lateral water movement occurs where percolating water meets a dense soil layer, i.e. a layer with high bulk density. Jordan (1970b) also investigated downward movement of radioactive ⁸⁵Sr and ¹³⁴Cs in the soil, using lysimeters located at litter level and at a 12.7 cm depth. After six months, less than one-third of either element had moved below the litter zone, showing that the litter layer can effectively trap certain minerals.

Odum et al. (1970) estimated, using four different methodologies, forest floor respiration and gase-

ous exchange in forest soils. Their estimates ranged from 2.4 to 10.6 g C/M²·day. Using the closed-box accumulation procedure with no fan, carbon dioxide concentration increased linearly with time over a 40 minute period. They also found that the respiration rate was linearly related to the flow rate of air across the forest floor.

There are few quantitative data concerning soil erosion losses in the Luquillo Experimental Forest or from other areas in Puerto Rico. Lewis (1974) showed that mass subsoil movement was substantial on certain soils in the Forest, even in soils having many fine rootlets. He attributed this phenomenon to expansion and contraction of soil particles between roots and effects of throughflow on underlying soil layers. Predictions of average annual soil loss in ton/ha are available for soil series in Puerto Rico by using the Universal Soil Loss Equation Model (USDA Soil Conservation Service 1978). The equa-

Table 15.—Selected profile and laboratory data for Múcara silty clay loam (fine, montmorillonitic, isohyperthermic Vertic Eutropept^a)

Horizon	Depth (cm)	Profile data								
		Texture			Organic carbon (%)	Nitrogen (%)	Water content 15–Bar (%)	pH (1:1 in H ₂ O)		
Sand (2–0.05)	Silt (0.05–0.002) (%)	Clay (<0.002)								
Ap	0–15	Very dark grayish brown (10YR 3/2) clay with few fine faint dark greenish gray (5BG 4/1) mottles; weak fine subangular blocky structure.								
B2	15–30	Brown (10YR 5/3) 60 percent and very dark grayish brown (10YR 3/2) 40 percent clay; weak medium subangular blocky structure.								
C	30–51	Semiconsolidated weathered volcanic rock. There are few stringers of A-C material running down into the saprolite.								
Ap	0–15	23.2	36.0	40.8	2.67	0.233	23.0	5.8		
B2	15–30	21.4	34.8	43.8	1.44	0.135	23.6	6.4		
C	30–51	0.10	10.9	6.6		
		Extractable bases				Cations exchange capacity		Base saturation		
		Ca	Mg	Na	K	Sum	Sum cations	NH ₄ OAc	Sum cations	NH ₄ OAc
		-----meq/100 g-----						-----percent-----		
Ap	0–15	27.0	14.4	0.2	0.3	41.9	54.2	42.9	77	98
B2	15–30	28.3	17.0	0.4	0.2	45.9	54.8	44.7	84	103
C	30–51	22.3	14.3	0.4	0.1	37.1	40.6	34.5	91	108

^aAdapted from U.S. Department of Agriculture, 1967.

Table 16.—Soil characteristics* at El Verde from July 28 to August 21, 1963. (Odum 1970a)

Measurement	Stations				
	1	2	3	4	5
Altitude (m)	343	406	469	538	603
pH (50% soil; 50% water)	5.0	4.9	5.1	5.1	5.0
Bulk density (g/ml)	0.87	0.74	0.83	0.71	0.72
Organic matter (%) [†]	5.8	9.8	11.2	5.4	9.8
Mechanical analysis:					
Sand (%) (2.0–0.05 mm)	28.4	18.4	32.4	36.4	30.4
Silt (%) (0.05–0.005 mm)	24.0	16.0	24.0	21.0	21.0
Clay (%) (<0.005 mm)	47.6	65.6	43.6	42.6	48.6
Crown height (m)	21.6	21.6	27.1	17.7	18.6
Palms (%)	30	0	10	25	15
Mean daily precipitation during the period, (cm)	1.32	0.86	1.02	1.30	1.63
Root depth (cm)	41	36	33	25	33
Soil moisture (gH ₂ O/g dry mass)					
July 28 [‡]	62	73	84	103	85
July 30 [‡]	78	82	67	87	97
August 5 [§]	67	62	75	97	86
August 9 [§]	68	57	62	80	84
August 15 [§]	66	68	75	94	83
August 21 [§]	65	61	69	85	94
Mean	68	67	72	91	88

*These characteristics were compiled by Weaver (1963) and Jagels (1963).

[†]Potassium dichromate method.

[‡]Each value is a mean of two determinations.

[§]Each value is a mean of four determinations.

Table 17.—Bulk density of the El Verde rain forest soil (Edmisten 1970d)

Horizon depth (cm)	Density (g/cm ³)		
	South control center	Radiation center	North cut center
0-15	1.05	1.18	0.66
15-30	1.02	1.14	0.92
30-61	1.00	1.11	1.03

Table 18.—Average infiltration rates for the El Verde rain forest soil (Edmisten 1970d)

Distance from center (m)	Average infiltration rates (min)*											
	North cut center				Radiation center				South control center			
	N	W	S	E	N	W	S	E	N	W	S	E
3	3	3	10	8	2 days†	3 days	191	2 days†	122	87	10	21
6	12	300	10	9	2 days†	1440	63	230	93	29	720	36
9	240	300	8	49	185	39	79	2 days†	12	18	680	2 days†
12	30	175	10	9	175	231	40	1000	69	67	10	240
15	220	36	7	10	780	60	40	1400	9	8	12	150
18	31	200	8	12	75	57	20	2 days†	8	7	11	255
21	28	15	200	15	25	9	18	27	10	32	40	740
24	19	180	102	108	28	10	40	28	14	58	28	15
27	300	15	11	12	25	7	38	25	6	10	15	10
30	8	10	7	12	10	40	126	35	12	7	11	7

*Average time in minutes for 7-cm head of water to infiltrate.

†The soil at these stations showed visible signs of foot trampling.

Table 19.—Chemical properties of Dominican and Puerto Rican soils (Soriano-Ressy et al. 1970)

Site*	Horizon (cm)	Cation-exchange capacity (meq/100 g)	pH	Exchangeable cations (ppm)				Absolute specific gravity (g/cm ³)
				Ca	Mg	K	Mn	
V-001	25 to 40	20.5	5.5	786	498	260	5	2.08
V-002	25 to 35	15.0	5.1	786	626	626	15	2.27
V-003	25 to 40	18.2	5.2	800	710	94	†	2.23
V-92‡	0 to 12	50.8	4.3	202	300	104	0.5	2.69
	12 to 25	11.2	4.3	270	87	24	0.5	
V-93‡	0 to 12	22.5	4.8	810	285	96	5	2.61
	12 to 25	11.6	4.9	415	99	24	†	
V-179	10 to 35	15.2	5.4	12	128	25	20	2.61
	35 to 65	15.4	5.4	150	215	35	†	
V-181	10 to 35	10.7	4.7	12	120	25	†	2.66
	35 to 65	12.8	4.8	58	89	45	10	

*V-001, V-002, V-003 are sites in Dominica.

†Not detected.

‡Obtained from Edmisten (1970d).

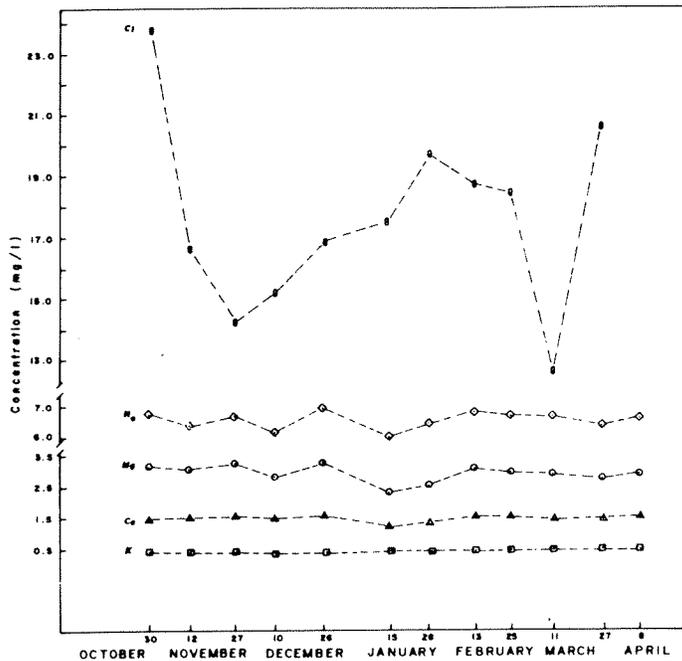


Figure 30.—Mean concentrations of chloride (Cl), sodium (Na), magnesium (Mg), calcium (Ca), and potassium (K) across time for stations on the Rio Espiritu Santo (Cuevas and Clements 1975).

tion incorporates six factors that influence soil erosion: rainfall intensity, inherent soil erodibility, slope length, slope percent, cropping management, and erosion control practices. Average annual soil loss per unit area is thus the product of all six factors. However, verification of predicted erosion losses to actual field losses within the Luquillo Experimental Forest have not been undertaken.

Existing soil physical data from the Luquillo Experimental Forest show that generalizations are impossible; each physical property is quite site specific, whether one is studying soil texture, bulk density, soil water movement, or gaseous exchange. Soil erosion processes are also complex and far from being fully understood. New insights could obviously be gained from additional studies on various soil physical parameters.

Chemical Properties

Data on chemical properties within the Luquillo Experimental Forest are more quantitative than data on soil physical properties. Soriano-Ressy et al. (1970) compared exchangeable cation values for El Verde and Sabana sites and found that they were lower than those of three soils from Dominica (table 19). Gruenwoldt (cited in Odum 1970a) measured

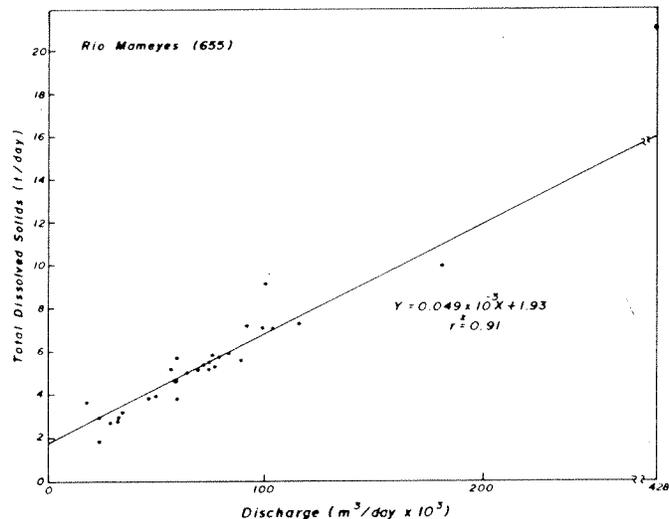
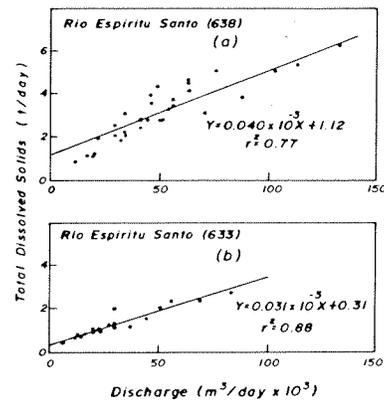


Figure 31.—Relation between stream discharge and export of total dissolved solids (original data are from U.S. Department of Interior, 1968–1976).

decreasing amounts of nitrogen, phosphorus, and potassium as soil depth increased; pH increased initially, and then decreased with depth (table 20). After treatment with radiation, soils at El Verde generally had lower element values than before radiation (Edmisten 1970d and table 21).

Wiegert and Murphy (1970) observed that leaf litter decomposition rates varied by tree species and by season (table 22). Wiegert (1970a) measured disappearance rates before and after radiation. He found that radiation did not seem to affect litter decomposition within the period of measurement.

Several papers have reviewed the effects of induced stressors, primarily radionuclides, on soil chemical properties. Kline and Odum (1970) found apparent accumulation of ^{144}Ce and ^{54}Mn but not of ^{137}Cs in forest litter from Puerto Rico and five other countries (table 23). Low-levels of ^{95}Zr – ^{95}Nb were found in the forests of all countries except one. Measurements of ^{137}Cs and ^{54}Mn , before and after radiation treatment at El Verde, showed no significant increase in leaching of these two elements from the forest can-

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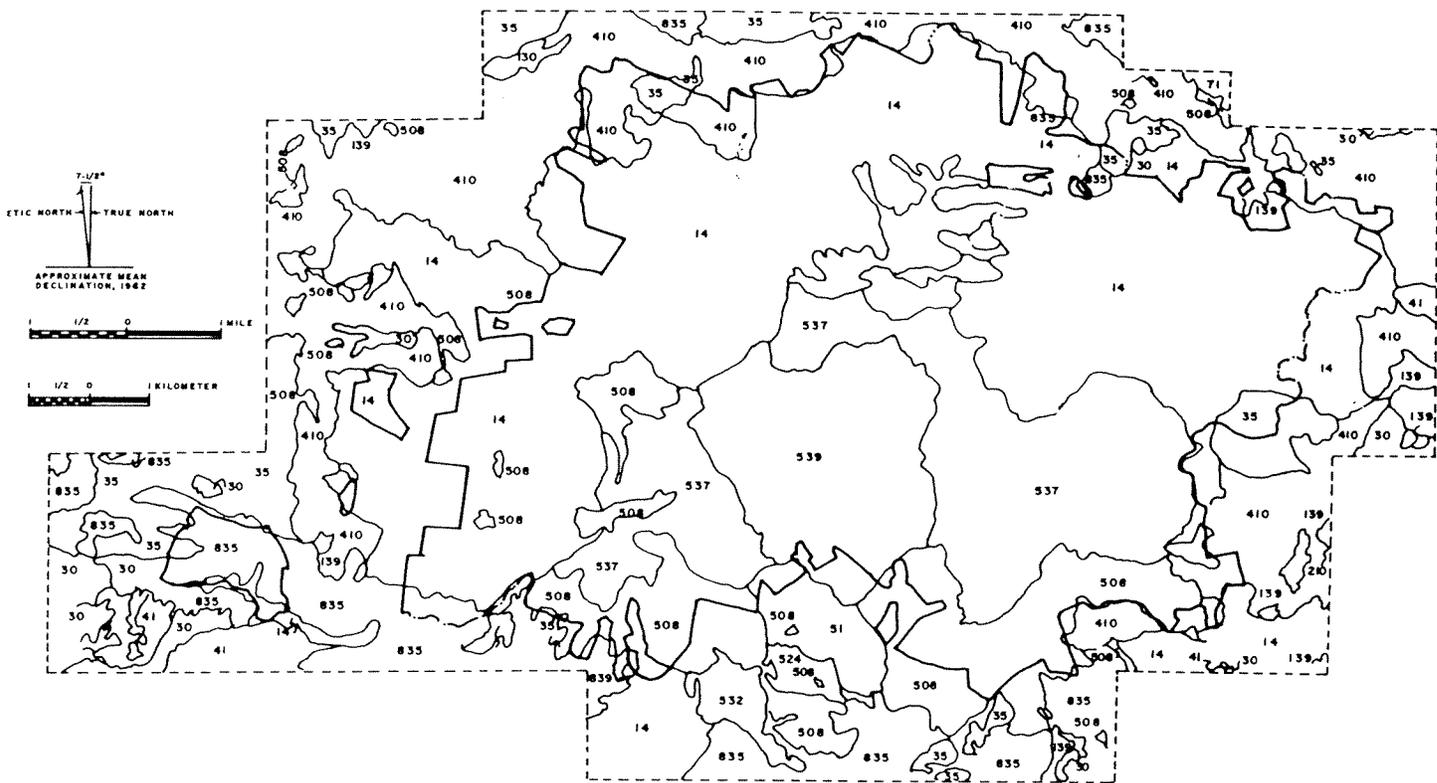


Figure 32.—Soil map of the Luquillo Experimental Forest. Key to symbols as follows:

Map Symbol	Soil Data	Soil Characteristics	Hazards and Limitations
14	Los Guineos clay and silty clay loam	Well drained and deep to volcanic rocks	Severe slopes, erosion hazard
30	Naranjito silty clay loam	Well drained and moderately deep to volcanic rock	Severe slopes, very severe erosion hazard, rapid runoff
35	Mucara silty clay	Well drained and moderately deep to volcanic rock	Severe erosion hazard, medium to very rapid runoff
41	Sabana silty loam	Well drained and shallow to volcanic rock	Severe slopes, severe erosion hazards, very rapid runoff
51	Pandura loam	Well drained and moderately deep to granitic rocks	Severe erosion hazard, very rapid runoff
139	Aceitunas silty clay loam	Well drained, deep and formed in moderately fine and fine textured sediments.	Moderate limitations for recreational uses, moderate erosion hazard
410	Humatas clay	Well drained and deep to volcanic rocks	Severe limitations for recreational uses and moderate or severe erosion hazard
508	Rock land	Shallow soil material found between outcrops with loose stones on surface	Type is limited to forest habitat for wildlife, and water catchment
524	Guayabota silty loam	Poorly drained and shallow to volcanic rocks	Severe limitations for recreational uses, medium to rapid runoff
537	Guayabota-Ciales-Picacho association	50% Guayabota soils and 20% Ciales soils	Continuously wet and unstable, slow permeability and susceptible to slippage
539	Utuaedo-Picacho-stony rock land association	40% Utuaedo soils, 25% Picacho soils and 20% stony rock land	Continuously wet and susceptible to slippage
71	Yunes silty clay loam	Shallow or moderately deep to volcanic rocks	Low available water capacity and susceptible to erosion
835	Caguabo clay loam	Well drained and shallow to volcanic rocks	Severe limitations for recreational uses and very rapid runoff

Table 20.—Chemical properties of a soil near El Verde in the Luquillo Experimental Forest (Odum 1970a)

Depth (cm)	Nitrogen (%)	Phosphorus (%)	Potassium (ppm)	pH
15*	2.12	0.022	44	4.25
61	0.67	0.023	10	4.80
122	0.32	0.037	10	4.50
244	0.32	0.38	44	4.60

*Data are taken from Gruenwoldt (1962).

Table 21.—Chemical properties of the upper soil layers of the El Verde rain forest before and after irradiation (Edmisten 1970d)

Horizon (cm)	Time	pH [†]	Acid-extr. P (ppm)	CEC* (meq/100 g)	Exchangeable portion (ppm)							
					Ca	Mg	K	Na	Zn	Cu	Mn	Fe
South Control Center												
0-13	Sept. 1964	4.3	21	50.8	202	300	104	†	0.5	0.5	0.5	†
	May 1965	4.2	26	52.3	216	311	98	†	0.5	0.5	162	†
13-25	Sept. 1965	4.9	16.5	24.8	248	262	134	182	0.1	5.0	75	50
	Sept. 1964	4.3	17	11.2	270	87	24	†	0.5	0.5	0.5	†
	May 1965	4.1	19	10.8	210	93	27	†	0.5	0.5	37	†
	Sept. 1965	4.7	12.5	12.2	165	127	14	453	0.1	1.0	25	60
Radiation Center												
0-13	Sept. 1964	4.8	21	22.5	810	285	96	†	0.5	0.5	0.5	†
	May 1965	5.6	37	24.8	1,160	380	121	†	3	1	58	†
13-25	Sept. 1965	4.7	16.5	20.5	440	237	48	182	17.8	1.0	185	75
	Sept. 1964	4.9	14	11.6	415	99	24	†	0.5	0.5	†	†
	May 1965	5.7	20	13.1	560	140	39	†	1	0.5	40	†
	Sept. 1965	4.8	14.5	11.7	220	127	18	345	15.7	1.0	35	75
North Cut Center												
0-13	Sept. 1964	5.7	13	29.1	3,840	1,515	186	†	0.5	0.5	170	†
	May 1965	6.1	18	36.7	3,900	1,640	280	†	4	1.0	182	†
13-25	Sept. 1965	5.7	12.5	25.3	1,650	704	76	242	17.8	1.0	575	125
	Sept. 1964	5.4	6	17.1	1,110	873	30	†	0.5	0.5	40	†
	May 1965	5.8	10	18.6	1,750	990	60	†	1.0	1.0	58	†
	Sept. 1965	5.2	6	17.6	907	683	26	363	8.7	1.0	625	125

*Cation exchange capacity.

†Not analyzed.

‡pH of soil mixed with water 1:1.

Table 22.—Litter disappearance rates by tree species at El Verde (Wiegert and Murphy 1970)

Litter type	Tree above bags					
	<i>Euterpe</i>	<i>Croton</i>	<i>Manilkara</i>	<i>Sloanea</i>	<i>Dacryodes</i>	<i>Cecropia</i>
<i>Euterpe</i>	1.775*	1.490	1.130	1.410	1.505	1.315
<i>Croton</i>	3.960	2.230	3.355	2.390	3.275	2.425
<i>Manilkara</i>	1.645	1.005	0.845	1.345	0.930	1.310
<i>Sloanea</i>	1.610	1.240	1.430	1.760	1.805	1.600
<i>Dacryodes</i>	2.225	1.710	1.365	1.500	1.945	1.275
<i>Cecropia</i>	1.515	1.095	1.300	1.445	1.965	1.540

*Each value is the mean of two stations and represents cumulative disappearance during two years.

Table 23.—Relative amounts of ^{144}Ce , ^{137}Cs , and ^{54}Mn in leaves and litter from Caribbean and Central American forests (Kline and Odum 1970)

Forest	^{144}Ce leaves*	^{137}Cs leaves†	^{54}Mn leaves‡
	^{144}Ce litter	^{137}Cs litter	^{54}Mn litter
Puerto Rico			
Limestone	0.4	0.8	0.6
Maricao [§]			
El Verde	0.8	1.6	0.9
Elfin	0.6	1.7	0.7
Other islands			
Dominica	0.4	0.7	0.4
Trinidad	0.6	0.8	0.2
Central America			
Costa Rica (Turrialba)	0.5	0.9	0.7
Costa Rica (Sarapiquí)	1.7	4.0	1.3
Panama (San Lorenzo)	0.7	1.0	0.7
Mexican (Uxmal, Yucatán)	0.5	3.0	

*Population < 1 at 94% confidence level by the Wilcoxon signed-rank test.

†Population not different from one by the Wilcoxon signed-rank test.

‡Population < 1 at 97% confidence level by the Wilcoxon signed-rank test.

§Litter sample not run.

Table 24.—Average elemental content (kg/ha) of major compartments of the rain forest at El Verde (Jordan et al. 1972)

Compartment	Ca	Na	K	Mg	Mn	Fe	Cu
Leaves	55	21	24	26	3.4	1.3	0.08
Woody materials	380	218	143	95	15.2	9.6	0.59
Litter	11	1	1	6	0.6	23.6	0.10
25 cm of upper mineral soil	176	156	31	155	3.4	28.5	0.19

opy to the forest floor (Kline et al. 1970). Kline (1970) noticed a doubling of environmental half-life of ^{95}Zr – ^{95}Nb , ^{144}Ce and ^{54}Mn as opposed to the normal physical half-life and some incorporation of these nuclides into the forest mineral cycle. Six months after application, Jordan (1970b) found that only about one-third of ^{134}Cs and ^{85}Sr had moved down from the forest litter to the 12.7 cm depth in zero-tension lysimeters. Kline and Mercado (1970) also demonstrated that forest litter layers might be an effective “sink” for radionuclides and other elements. They found that plants had taken up only 1% of ^{134}Cs and ^{54}Mn one year after their application; the remainder was in the top 10 cm of soil. Six herbicides applied to soils west of El Verde produced no sterilization effect and the forest floor was covered with grasses, sedges, and vines within one year of treatment (Dowler and Tschirley 1970).

Jordan et al. (1972) and Odum (1970b) reviewed existing knowledge and hypotheses about nutrient

budgets and general cycling pathways within the Luquillo Experimental Forest. There are relatively large pools of certain elements like calcium, sodium, magnesium, and iron in the soil as compared to the vegetation pools. For other elements, storage pools in the soil are relatively low (table 24).

Some studies exist for specific elements. Odum et al. (1970) and Bloom and Raines (1970) developed models for the hydrogen budget. Most hydrogen is located in soil water in the forest litter and upper soil. An estimate of hydrogen incorporated into the organic state was $2.2 \text{ g/m}^2\cdot\text{day}$. Significant tritium remained in litter and top 18 cm of the soil seven months after its initial application (Kline and Jordan 1970).

Luse (1970) studied the phosphorus cycle at El Verde. He observed little phosphorus migration in the soil, either laterally or vertically, after applying ^{32}P into injection holes in two tree species. The concentration of phosphorus in organic matter in contact with roots was 1.34 mg/g , compared to a concentration of 0.66 mg/g in the roots.

Edmisten (1970e) summarized the nitrogen cycle at El Verde. Mean Kjeldahl nitrogen concentration in soil water increased with depth in the soil profile (table 25). Losses from the soil via denitrification ($1.7 \text{ g/m}^2\cdot\text{yr}$) were higher than losses via runoff ($0.9 \text{ g/m}^2\cdot\text{yr}$) (Edmisten 1970e). His measurements suggested that epiphytes and soil fungi can make considerable contributions to the overall nitrogen cycle.

In summary, baseline soil chemical data exist for several sites within the Luquillo Experimental Forest, particularly at El Verde. They cover such

areas as nutrient concentrations in different soil horizons, litter decomposition rates, and influence of certain stressors like radionuclides.

Biotic Properties

Various animal groups have been studied in the Forest. Weigert (1970b) showed that termite (*Nasutitermes costalis* (Holmgren)) numbers per nest are related more to nest surface area rather than nest volume, perhaps because respiratory gas exchange must occur by diffusion through the nest surface. After radiation treatment, irradiated nests had less biomass of various termite life stages than did the control area (table 26). McMahan (1970) found that *N. costalis* was quite sensitive to radiation, being perhaps more sensitive than other insects of comparable size.

Stiven (1970) estimated biomass of four snail species in forest litter samples at 9.5 g/m². He also observed that niches of El Verde gastropods were non-overlapping and contiguous, a phenomenon in agreement with other ecological observations elsewhere. Litter inhabiting gastropods might play a significant role in litter turnover, either directly through grazing or indirectly by feeding on litter microbial populations

Moore and Burns (1970) estimated fresh weight of earthworms from six pits at El Verde to be 43.1 g/m². They stated that earthworms were the most important animal fraction on a weight basis.

In study of microarthropods, McMahan and Solins (1970) identified 313 species at the El Verde site (fig. 33). Species diversity, calculated several different ways, was always high. No change in species diversity appeared after radiation. Wiegert (1970b) also saw no adverse effects of radiation on microarthropod fauna in either litter or soil layers; the soil could actually have been an effective shielding mechanism.

Numbers of nematodes at El Verde were approximately three times higher in soil than in litter layers (table 27). The values in soil are much lower than those for temperate grassland or forest areas (Coleman 1970). Biomass estimates, however, were higher in El Verde forest than in temperate areas. Biomass was 8 to 10 mg/m² in El Verde versus 1 to 10 mg/m² in temperate areas.

Cowley (1970a) identified at El Verde 66 different fungal species before radiation and 98 species afterwards (tables 28 and 29). He suggested that population changes were probably due to increased canopy exposure and subsequent substrate changes rather than to direct radiation effects. Edmisten

Table 25.—Elemental nitrogen in rain forest waters at El Verde (Edmisten 1970e)

Type of composite sample	N(ppm)				Mean
	December 1968*	January 1969*	First week Feb. 1969	Second week Feb. 1969	
Rainwater, above canopy	0.56	0.32	0.52	0.44	0.46
Throughfall, after hitting leaves	0.64	6.63	2.22	1.71	2.80
Stemflow	7.36	0.96	1.32	2.89	3.13
Soil water, below litter	1.38	1.18	2.33	1.26	1.54
Soil water 15 cm deep, A horizon	7.53	1.17	0.99	0.82	2.63
Soil water, 60 cm deep, B horizon	3.90	NS [†]	9.43	NS [†]	6.67
River water	2.66	1.20	0.29	0.73	4.88

*Entire month.

[†]No sample.

Table 26.—Number and biomass of termites (*Nasutitermes costalis*) in the radiation and south control centers at El Verde (Wiegert 1970b)

	Workers	Soldiers	Nymphs	Eggs	Total
No/m ² :					
South Control Center	80	15	9	14	118
Radiation Center	68	12	7	12	99
Mg dry mass/m ² :					
South Control Center	68.8	5.4	0.9	0.3	75.4
Radiation Center	58.5	4.3	0.7	0.2	63.7

Table 27.—Number of nematodes present in the rain forest at El Verde (Coleman 1970)

	\bar{X}	SD	N	No./m ²
South Control Center*				
Litter	5.6	4.2	5	2,200
Soil	14.8	2.9	5	5,900
Total	20.4			8,100
Radiation Center*				
Litter	6.0	4.2	4	2,400
Soil	16.4	8.8	5	6,600
Total	22.4			9,000
North Cut Center*				
Litter	13.2	7.9	5	5,300
Soil	46.6	63.9	5	19,000
Total	59.8			24,300

*Comparison of mean number of nematodes per 25 cm² core in: (a) South Control and North Cut Centers $\chi^2 = 96.8$, one degree of freedom, $p < 0.01$ (b) South Control and Radiation Centers $\chi^2 = 2.92$, one degree of freedom, $p < 0.10$.

(1970c) found that only 9 of 35 tree species had no mycorrhizal associations (table 30). Both species of tree and radiation influenced microfungal litter populations (Cowley 1970b; Holler and Cowley 1970; Witkamp 1970 and tables 31 and 32). Control plots had significantly higher numbers of fungi and bacteria than radiated plots. Tropical areas appeared to have fewer myxomycetes than do temperate areas (Alexopoulos 1970).

Several papers have outlined the diversity of invertebrate, micro and macro-arthropod, fungal, and bacterial populations found at the El Verde site, both before and after radiation experiments. Several of these initial studies revealed similarities between temperate and tropical populations and ecological processes, including earthworm numbers and herbivore grazing rates. Yet, there were noticeable dissimilarities between the El Verde site and certain temperate areas, at least for nematode numbers and myxomycete populations.

Root Profiles

Root and soil profiles at various sites in the Luquillo Experimental Forest have been described by Odum (1970a) and some examples are shown in figures 34–37. Soil under the dwarf forest (fig. 34a) is slightly acidic and reduced to a depth of about 40 cm at the boundary of the yellow and red clay. The number of roots declines rapidly with depth, the majority being located in the reduced zone. The soil organic layer in the dwarf forest meadow is clearly separated by a hardpan from the mineral layer (fig. 34b). The hardpan distinctly separates the reduced organic ooze from the oxidized zone.

Table 28.—Distribution of fungus fruiting bodies in major taxonomic groups of fungi at El Verde (Cowley 1970a)

	Percent of species		Percent of fruiting bodies	
	1964	1965	1964	1965
Gastromycetes	3	2	3	3
Hymenomycetes	82	68	74	55
Heterobasidiomycetes	3	2	2	<1
Ascomycetes	9	20	20	40
Slime molds	3	7	1	1

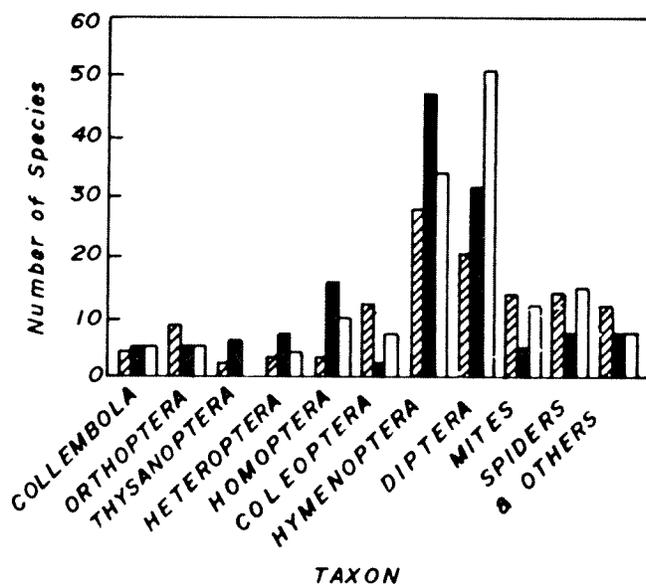


Figure 33.—Number of species in each major invertebrate taxon for the centers studied at El Verde. Larvae and hemipteran nymphs not included (McMahan and Sollins 1970).

In the lower montane forest, root numbers decrease with depth in the soil, but roots penetrate to greater depths than in the dwarf forest (fig. 35a–d). The number of roots rapidly decreases at the boundary between the organic and mineral layers. Fewer roots were found at sites with a thin organic layer (fig. 35c–d). Root numbers in well drained soils (fig. 36a–b) followed the same trend measured for the other pits (c.f. fig. 35a–d). Poorly drained soils (fig. 36c–d) had higher numbers of roots at greater depths than the well drained sites. Figure 37a–c, showing the same general trend measured for the other pits (figs. 34–36), is included to illustrate the variation in the soil profile and the resulting variation in root numbers.

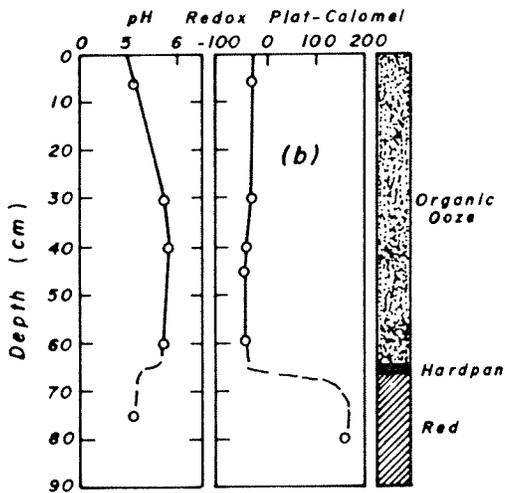
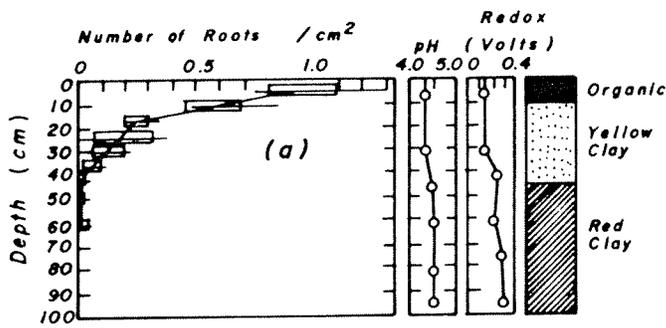


Figure 34.—Soil profiles of (a) dwarf forest and (b) dwarf forest meadow, both at Pico del Este (Odum 1970a).

VEGETATION

The four forest ecosystems found in the Luquillo Experimental Forest are the tabonuco, colorado, palm and dwarf forests (Wadsworth 1951; fig. 38). These four ecosystems are roughly stratified by altitude. The tabonuco forest is found below 600 m and is best developed on low, protected, well-drained ridges. This forest occupies nearly 70% of the Luquillo Experimental Forest. Above the average cloud condensation level (600 m) is the colorado forest which covers about 17% of the Luquillo Experimental Forest. Because of abrupt changes in topography and substrate, the tabonuco and colorado forests are often located within short distances of each other. On peaks and ridges above 750 m in elevation (2% of the Luquillo Experimental Forest) is the dwarf forest with its short, gnarled vegetation. The palm forest or palm-brake, interspersed within both the colorado and dwarf forests, covers 11% of the Luquillo Experimental Forest. This forest is limited to areas of steeper slopes, poor drainage and saturated soils. Almost pure stands of the sierra palm, *Prestoea montana* (Graham) Nichols (or earlier *Euterpe globosa* Gaertn), predominate in this forest type.

Table 29.—Diversity indexes for fungus fruiting bodies in various areas studied at El Verde (Cowley 1970a)

	Number of species	Number of fruiting bodies	Diversity index
1964 Radiation Center	43	148	19.82
1964 South Control Center	47	220	20.09
1965 Radiation Center	63	610	22.58
0 to 10 m	30	206	12.99
10 to 30 m	51	404	19.54
1965 South Control Center	60	607	21.51
0 to 10 m	40	242	16.80
10 to 30 m	43	365	16.81
1965 North Cut Center	30	444	11.32

Table 30.—Types of mycorrhizal associations of roots taken from El Verde trees (Edmisten 1970c)

Name	Type*	Confirmed slides
<i>Buchenavia capitata</i>	Endo.	4
<i>Casearia arborea</i>	Endo.	3
<i>Cyathea arborea</i>	Int.	5
<i>Cordia borinquensis</i>	Endo.	2
<i>Cananga caribaea</i>	—	0
<i>Croton poecilanthus</i>	—	0
<i>Cecropia peltata</i>	Ecto.	5
<i>Cyrilla racemiflora</i>	—	0
<i>Dacryodes excelsa</i>	Endo.	2
<i>Drypetes glauca</i>	Int.	5
<i>Didymopanax morototoni</i>	Ecto.	3
<i>Euterpe globosa</i>	Ecto.	4
<i>Ficus crassinervia</i>	Endo.	3
<i>Hirtella rugosa</i>	Int.	2
<i>Homalium racemosum</i>	Endo.	4
<i>Ixora ferrea</i>	—	0
<i>Inga laurina</i>	Ecto.	4
<i>Inga vera</i>	Ecto.	4
<i>Mayapea domingensis</i>	—	0
<i>Myrcia deflexa</i>	Int.	4
<i>Matayba domingensis</i>	Endo.	3
<i>Micropholis garciniaefolia</i>	Endo.	2
<i>Meliosma herbertii</i>	—	0
<i>Manilkara bidentata</i>	Endo.	3
<i>Magnolia splendens</i>	Endo.	4
<i>Miconia tetrandra</i>	—	0
<i>Ormosia krugii</i>	Ecto.	5
<i>Ocotea portoricensis</i>	—	0
<i>Palicourea riparia</i>	Endo.	5
<i>Rourea glabra</i>	Int.	4
<i>Sloanea berteriana</i>	Endo.	5
<i>Tetragastris balsamifera</i>	—	6

*Abbreviations: Endo., endotrophic mycorrhiza; Ecto., ectotrophic mycorrhiza; Int., intermediate condition. A dash indicates a lack of fungal tissue. The number of confirmed associations out of five slides prepared is noted in the last column.

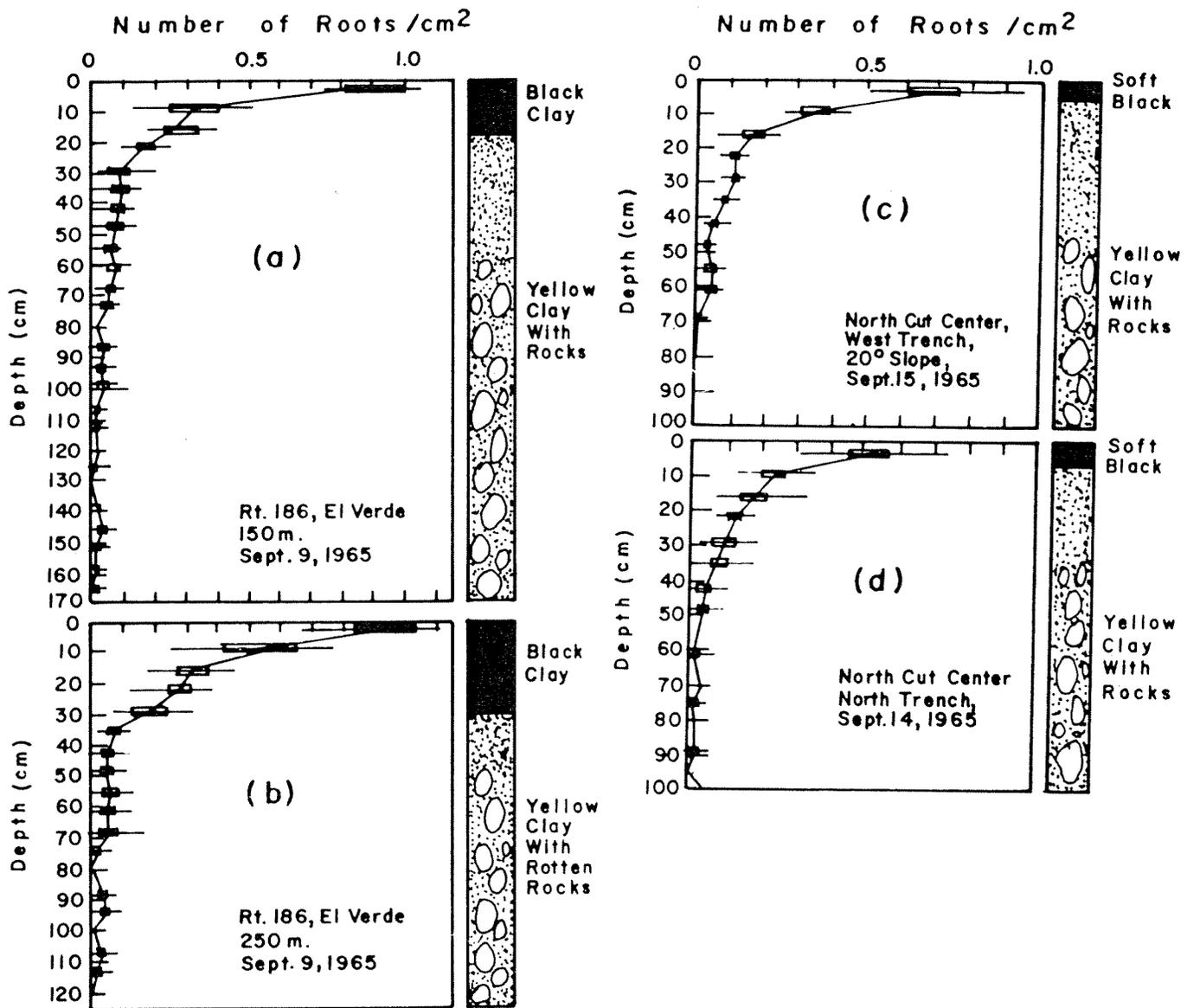


Figure 35.—Soil and root profile of the tabonuco forest at El Verde. Boxes represent one standard error above and below the mean and horizontal lines represent the range (Odum 1970a).

An increase in elevation in the Luquillo Mountains is accompanied by changes in climate and soils (discussed earlier) and also by variation in structure and species composition of the vegetation. Tree height, number of species, basal area, average tree dbh (diameter at breast height) and complexity index decrease with increasing elevations and only stem density increases (fig. 39). In general, vines and lianas become less common and epiphytes more common with the same altitudinal increase (White 1963).

The environmental characteristic most closely related to the occurrence of the tabonuco and colorado forests has been found to be impeded soil drainage (Wadsworth and Bonnet 1951). As soil becomes wetter, drainage poorer, and organic matter content greater with increasing altitude, roots form a more

surficial network (fig. 40). From a functional standpoint this aboveground root structure, as well as the abundant epiphytic growth, may play an important role in maintaining tight mineral cycles particularly in the colorado and dwarf forest where transpiration rates are low and precipitation and run-off are high (Odum 1970a).

Floristic Studies

The flora of the Luquillo Mountains has been the subject of investigation since as early as the middle of the nineteenth century. Outstanding among the earlier botanical collections was that of Eggers (1883). However, the most extensive collections of spermatophytes to date were made early in this century by Britton and Wilson (1923-30). Seavers and

Table 31.—Microbial characteristics of irradiated and nonirradiated Puerto Rican forests (Witkamp 1970)

Date	Location	Irradiation	Organic matter (%)	Moisture (%)	Fungi (10 ⁴ /ml)	Bacteria (10 ⁶ /ml)	CO ₂ evolution ml/m ² ·hr	O ₂ uptake μl/ml·hr
December 1964	10–140 m*	Preirradiation	43	57	240	45	21	35
	10–140 m	Preirradiation (behind rock)	41	58	134	41		31
April 1965	10–140 m	Exposed	51	62	12	7	38	32
	10–140 m	Shielded (behind rock)	40	65	15	34		33
	3–10 m	Exposed	60	69	3	96	24	46
	Control	None	43	52	34	30	18	32
November 1965	10–140 m	Exposed	56	67	130	200	63	31
	3–10 m	Exposed	40	58	131	142	88	39
	Control	None					57	
May 1966	10–140 m	Exposed	58	61	48	531	48	28
	3–10 m	Exposed	38	59	95	276	38	22
November 1965	Cut Center	None					141	
	East Peak (cloud forest)	None					46	
December 1964	El Toro (cloud forest)	None	92	82	68	12		27
	10–140 m (subsoil)	Shielded (by topsoil)	27	47	4	9		14

*Leaves remaining at 10 to 140 m from source and defoliated at 2.5 to 10 m from source after irradiation (January to April 1965.)

Table 32.—Microfungal species distribution among soil and litter layers at El Verde (Holler and Cowley 1970)

	Pre-irradiation	Post-irradiation
Number of species isolated from:		
Soil only	45	53
Root layer only	40	59
Litter only	41	53
Soil and roots but not litter	9	15
Soil and litter but not roots	14	9
Roots and litter but not soil	6	6
All three layers	6	4

Table 33.—Number of tree species found in the Luquillo Experimental Forest (Little & Woodbury 1976)

Forest type	Number of species
Tabonuco	153
Colorado	101
Palm	26
Dwarf	43

Chardón (1926) collected fungi, and later, Crum and Steere (1957) described mosses from the Luquillo Mountains. Liogier (1965) has since revised the nomenclature of the flora of Puerto Rico. Specimens from these collections are now catalogued in the herbarium of the University of Puerto Rico's Agricultural Experiment Station and are updated and added to continuously. Herbariums are also maintained at the Institute of Tropical Forestry in San Juan and the El Verde Field Station in the Luquillo Experimental Forest. More recently, Little and Wadsworth (1964) and Little et al. (1967) described 750 common trees of Puerto Rico. Illustrated keys for the identification of seedlings and leaves of many of these species have been constructed by Duke (1965) and Smith (1970). In addition, Kepler (1975) has described and constructed taxonomic keys for the ferns and fern-allies of the Luquillo Mountains.

Little (1970) and, more recently, Little and Woodbury (1976) list the trees of the Luquillo Experimental Forest and the forests in which they occur (table 33). They reported 225 woody species in 144 genera and 59 families, of which 178 are native and 47 introduced. Many of the 47 introduced species have been planted for stabilization of roadsides and slopes (e.g. bamboo, *Bambusa vulgaris* Schrad.) and

Table 34.—Summary by ranges of native tree species of the Luquillo Experimental Forest and Luquillo Mountains (Little and Woodbury 1976)

Also on continent, 91 species, 41%
(1) Puerto Rico to both South America and Central America or also Mexico or Florida), 63 species, 28%
(2) Puerto Rico to South America (including Panama) only, 21 species, 10%
(3) Puerto Rico to Central America (or Mexico or Florida) only, 7 species, 3%
West Indies but not continent, 64 species, 28%
(4) Greater and Lesser Antilles only, 31 species, 14%
(5) Greater Antilles only, 25 species, 11%
(6) Puerto Rico and Lesser Antilles only, 8 species, 3%
Endemic to Puerto Rico (or also Virgin Islands) (E), 70 species, 31%
(7) Puerto Rico and Virgin Islands only, 2 species, 1%
(8) Puerto Rico only (but not confined to Luquillo Mountains), 45 species, 20%
(9) Luquillo Mountains only, 23 species, 10%

Table 35.—Rare and endangered plants found in the Luquillo Experimental Forest (Woodbury et al. 1975)

Plant	Endangered endemic	Rare endemic	Endangered nonendemic	Rare nonendemic
Herb-vine	1	1
Tree	21	8	10	13
Shrub	4	5
Herb	2	5	3
Epiphytes-orchids	3	6	2
Epiphytes-other	3	2
Woody-vine	1	2
Sedge	3	2
Grass	2	5

in forestry plantations (e.g. Kadam, *Anthocephalus chinensis* Miq).

The Luquillo Experimental Forest has the largest number of rare species of any forest in the National Forest system. Sixty-eight species have been classed as endemic to Puerto Rico and of these 23 are found only within the boundaries of the Forest (table 34). A publication concerning rare and endangered plants of Puerto Rico (Woodbury et al. 1975) includes these tree species and expands the list to include species of other forest strata, e.g. orchids, herbs, and vines, for a total of 98 species which may be considered rare or endangered in the Luquillo Mountains (table 35). The large proportion of endemic species in the flora is evidence of the effect of age, isolation, and size of the island upon plants. In addition, the Luquillo Mountains may be considered a 'climatic island' within an island as is evident from the existence of pairs of parallel endemic species in the eastern and western mountains of Puerto Rico (Little 1970).

Autecological Studies

Comprehensive autecological studies have been conducted on six species, five trees and one shrub, in the Luquillo Experimental Forest: the sierra palm (Bannister 1970), *Palicourea riparia*, a shrub, (Lebrón 1977), *Inga vera* (Muñiz-Meléndez 1978), *Cecropia peltata* (Silander 1979), *Buchenavia capitata* (Sastre-DeJesús 1979), and *Didymopanax morototoni* (Nieves 1979). Studies such as these, which focus on processes and survival at different life stages, permit a comparison of life history strategies. The life history of the sierra palm, dominant in the palm forest, has been discussed in the corresponding section.

Of the four canopy trees, both *Didymopanax morototoni* and *Cecropia peltata* are early successional species, whereas *Inga vera* and *Buchenavia capitata* have characteristics more similar to those of late secondary or primary species. Germination of *Cecropia* occurs only in response to the creation of light gaps and appears to be inhibited by the predominant far-red light on the forest floor (Silander 1979). Both *Cecropia* and *Didymopanax* are dispersed widely by many species of birds which frequent both openings and forested areas. Thus seeds may be present in the soil and available for germination prior to the creation of a gap or may arrive soon after. Seeds of secondary species are normally attributed with long viability on the forest floor. However, both Nieves (1979) and Silander (1979) found that longevity may be low as a result of insect predation in the soil. Height growth of both species is initially rapid, and reproductive maturity is reached early, approximately 5 to 6 yr in *Cecropia* and 10 yr in *Didymopanax*. Flowering and fruiting occurs year round, typical of successional species, but peaks in

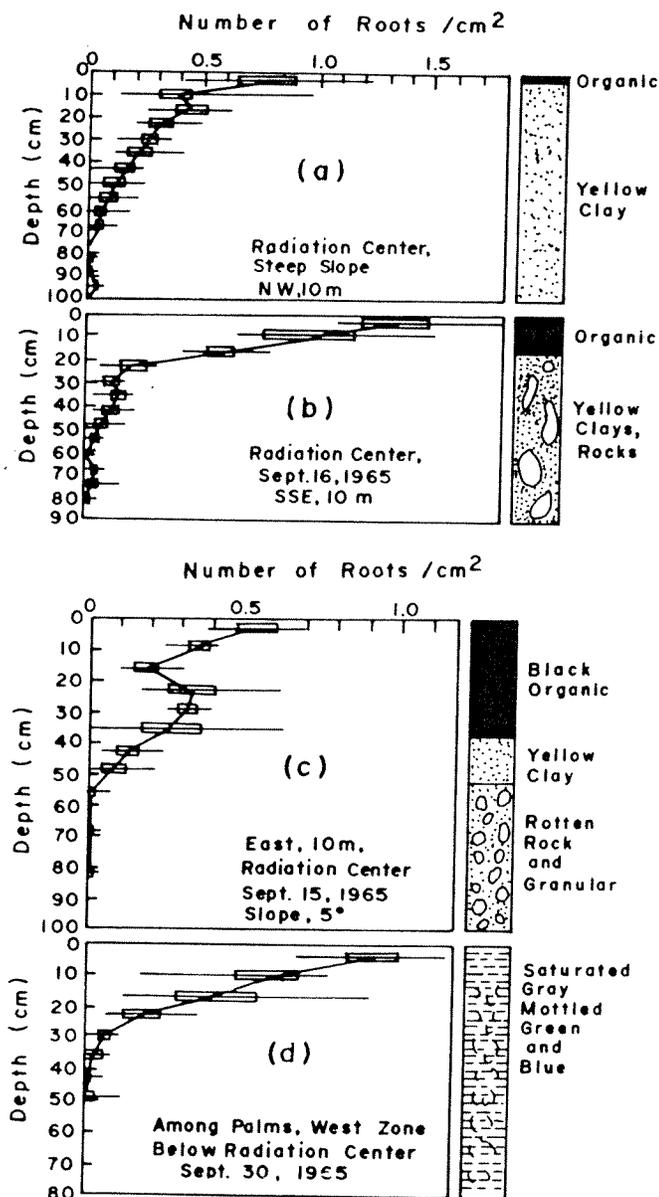


Figure 36.—Soil and root profiles of (a) and (b) well drained and (c) and (d) poorly drained locations at El Verde. Boxes represent one standard error above and below the mean and horizontal lines represent the range (Odum 1970a).

both species occur in the drier months of the winter season. Seed production by both species is profuse throughout the relatively short reproductive lifetime.

Mortality in *Cecropia* was greatest in the seed and seedling stages. However, in both *Inga* and *Buchenavia*, the greatest mortality occurred in the young tree or sapling stage. As with *Palicourea*, *Inga* and *Buchenavia* germinate both in the forest and in openings. Their growth and survival are enhanced under open, sunny conditions. Seedlings may, however, survive for long periods of time within the forest. Seeds of *Inga* and *Buchenavia* are larger and seed produc-

tion lower than the production by *Cecropia* and *Didymopanax Buchenavia*, one of the few deciduous species in the forest, drops its leaves all at once, and flowers immediately thereafter. This species has been reported to be one of the fastest growing trees in the forest (Sastre 1979).

In addition to these complete autecological studies, other workers have reported on specific aspects of the life history of plants in the Luquillo Experimental Forest. For example, Edmisten conducted studies on *Phytolacca icosandra* (1970b) and *Ormosia krugii* (1970a) seedlings; Koo and Venator (1970) studied growth of bromeliads; and Quarterman (1970) worked on the germination of three species: *Dacryodes excelsa*, *Linociera domingensis*, and *Smilax coriacea*.

Lugo (1970) found three photosynthetic strategies in successional and climax species (table 36): 1) early successional species, like *Cecropia*, were characterized by net photosynthesis: night respiration ratios (P/R) greater than 1; 2) climax species, such as *Sloanea*, exhibited P/R of 1 and their seedlings responded to sunflecks with fast photosynthetic rates but with net respiration during cloudy days; and 3) species such as *Dacryodes* with P/R of less than 1 and its seedlings which could not survive for long periods of time on the forest floor. Half-life determination of seedlings yielded 7.5–8.5 months for *Dacryodes* (Lugo 1970), 17 months for the sierra palm (Bannister 1970); and an average of 6 months for all forest species (Smith 1970b).

Tabonuco Forest

Physiognomy.—Occupying the greatest land area and the subject of extensive ecological studies by a variety of institutions is the tabonuco forest. The dominant tree, tabonuco (*Dacryodes excelsa* Vahl), from which the forest derives its name, often comprises as much as 35% of the forest canopy (Wadsworth 1951). Best developed on low, protected, well-drained ridges below 600 m, this forest exhibits many of those characteristics so frequently attributed to tropical rain forests. Three tree strata are obvious: a discontinuous upper stratum, a second continuous canopy at 20 m, and understory. The forest floor beneath these three strata is only sparsely vegetated. The open appearance of the tabonuco forest, in contrast to other types in the Luquillo Experimental Forest, is accented by the lack of branches to heights greater than half the height of most trees. A second predominant tree, motillo (*Sloanea berteriana* Choisy), bears the characteristic large rain forest buttress roots useful in the support of a large crown in saturated soil. Bromeliads, lianas, vines,

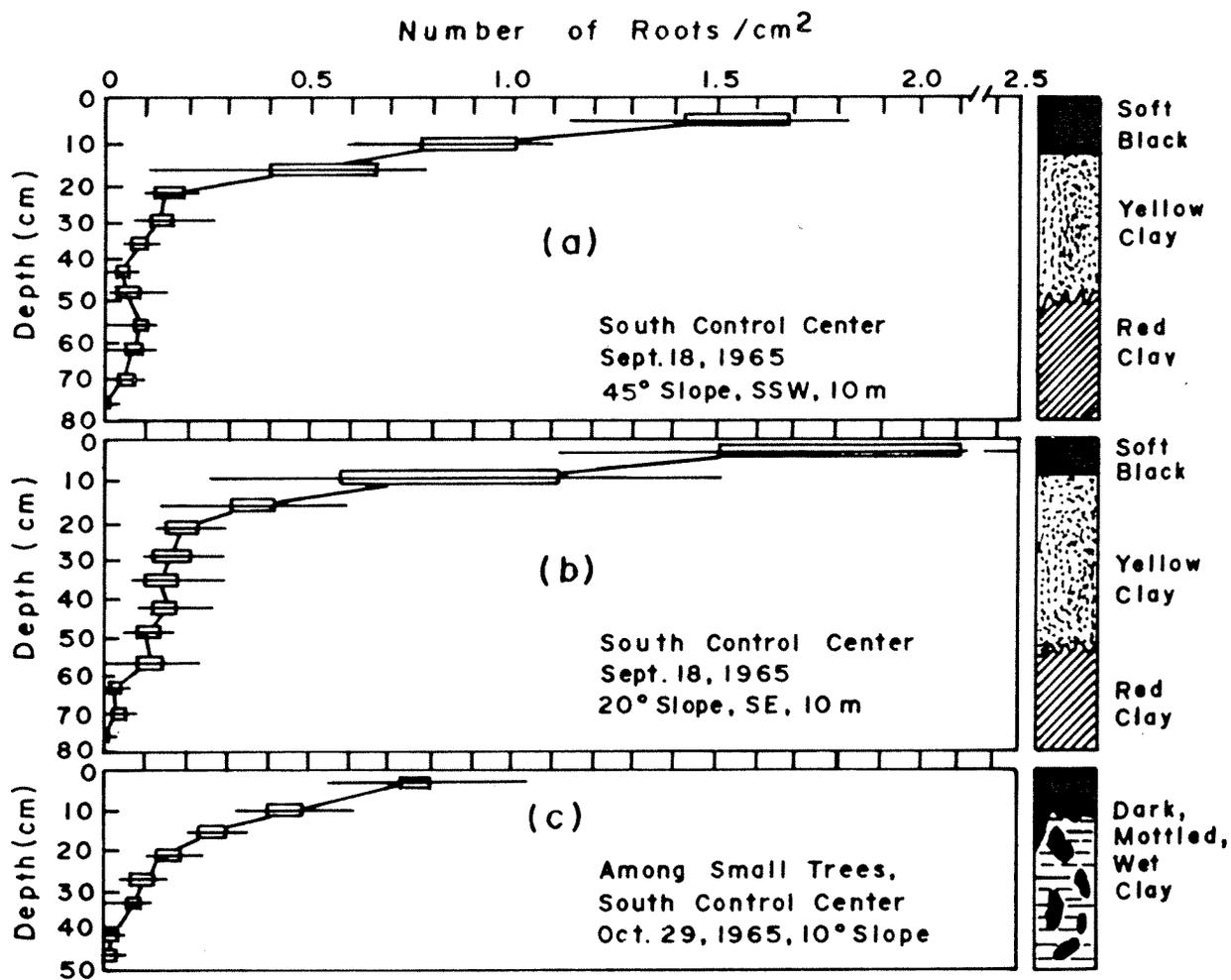


Figure 37.—Soil and root profiles of the tabonuco forest at El Verde. Boxes represent one standard error above and below the mean and horizontal lines represent the range (Odum 1970a).

and arborescent ferns are frequently observed. Leaves are mesophyllous, and shade leaves, often different morphologically from sun leaves, tend to be covered with epiphytic growth.

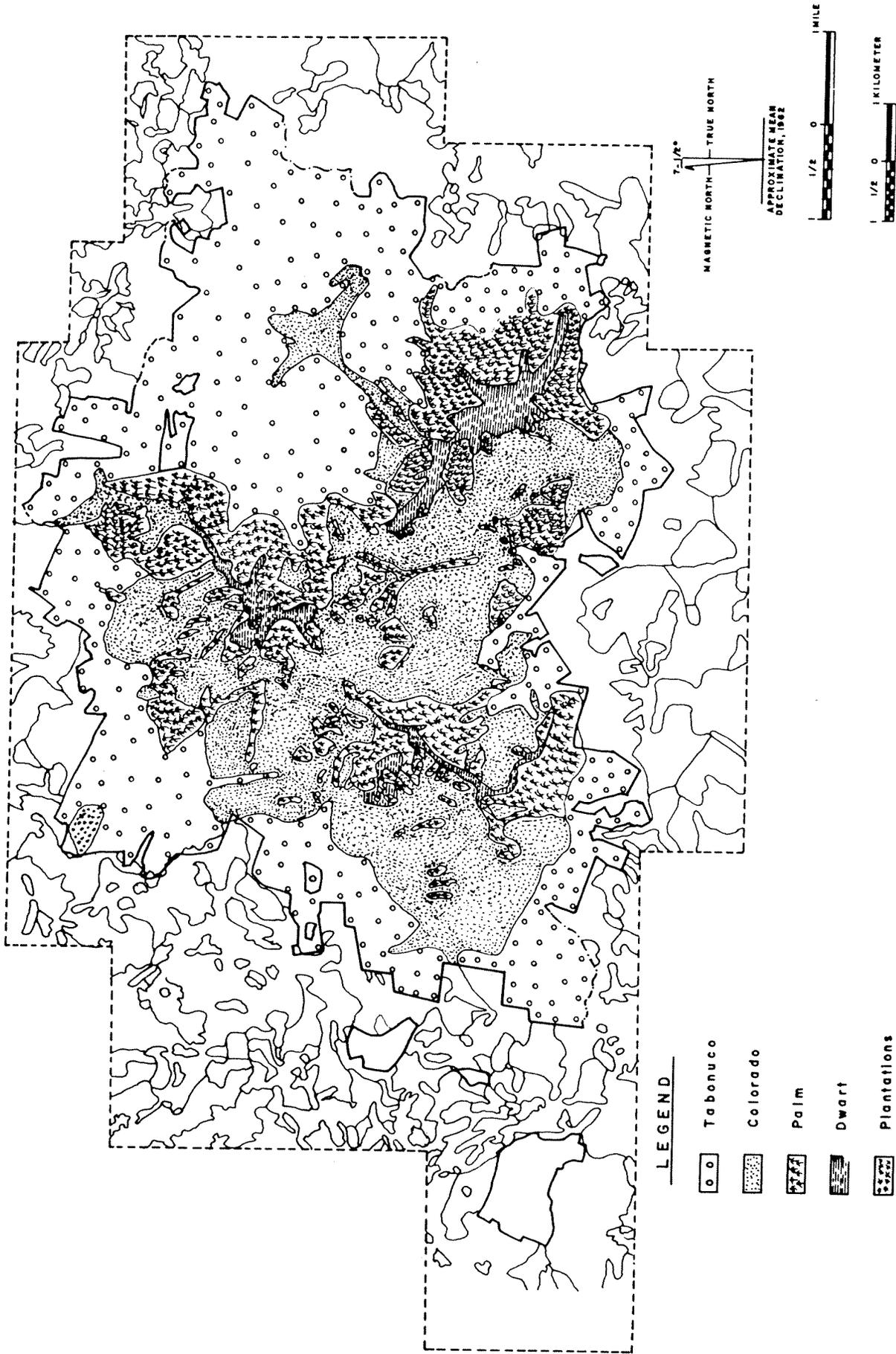
Wadsworth (1951) reported 168 species of which only 13 are deciduous, in the tabonuco forest. The size class distribution and frequency of 34 common species in the virgin forest are shown in table 37. The sierra palm and *Cecropia peltata* L., a successional species, are most numerous but their diameters rarely exceed 25 cm. Tabonuco is the third most common tree, but has the greatest number of trees in the largest size class. Tabonuco is ranked number one on the basis of density, basal area and volume (table 38). Most conspicuous in the understory of the tabonuco forest, the palm is ranked second and *Cecropia* is third. Indicator species of the tabonuco forest are listed in table 39.

The most extensive ecological study of the tabonuco forest was the Rain Forest Project of the U.S. Atomic Energy Commission (U.S. AEC) from 1963

to 1968. Project objectives were evaluation of the effects of prolonged gamma irradiation upon the forest and, simultaneously, increasing the understanding of the structure and functioning of the rain forest system. Studies, conducted at numerous locations within the forest, were concentrated near the El Verde Field Station at an elevation of 355 m (fig. 3). Throughout the study, individual experiments carried out by a wide variety of resident and visiting scientists contributed to the information required to understand structure, both horizontal and vertical, and various system processes including mineral cycling, energy flow and forest regeneration mechanisms.

Floristic studies measured the relative densities of species found in each forest synusia: canopy, understory, climbers, stranglers, epiphytes, herbs, saprophytes and semiparasites (table 40). In an area of 2 ha a total of 214 species in all synusia were reported (Smith 1970b). Almost half of the understory was composed of a single species, *Palicourea riparia* Benth., with a relative density of 41.5%. Absolute

LUQUILLO EXPERIMENTAL FOREST



LEGEND

- Tabonuco
- Colorado
- Palm
- Dwarf
- Plantations

Figure 38.—Vegetation map of the Luquillo Experimental Forest.

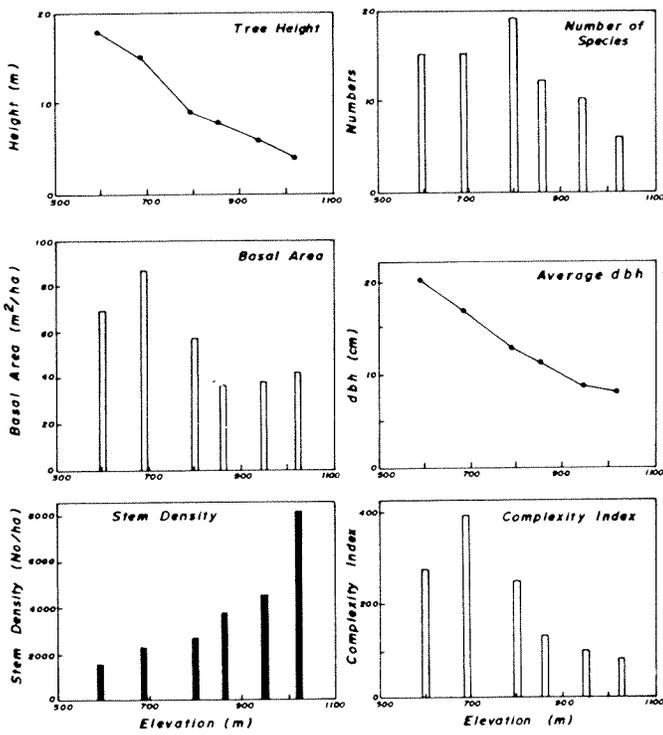


Figure 39.—Variation of stand structure, diversity, and complexity index (Holdridge et al., 1971) of the four forest types in the Luquillo Experimental Forest (adapted from White 1963).

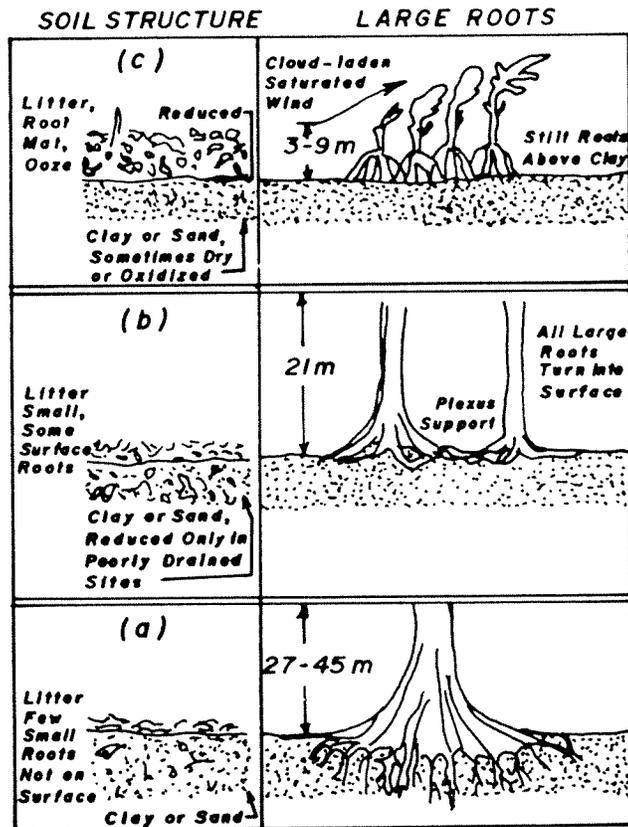


Figure 40.—Differences in soil structure and roots with increasing altitude in (a) dwarf forest, (b) tabonuco or lower montane, and (c) lowland forest (Odum 1970a).

Table 36.—Summary of metabolic characteristics of four species studied in the tabonuco forest at El Verde (Lugo 1970)

Species	Conditions	Av. max. rate of net photosynthesis (g C/m ² -hr)	Av. max. rate of night respiration (g C/m ² -hr)	Av. compensation point (g-cal/cm ² -min)	Av. saturation point (g-cal/cm ² -min)	Av. peak or point (g-cal/cm ² -min)	Av. rate of net photosynthesis (g C/m ² -hr)	Av. rate of night respiration (g C/m ² -hr)	Av. total net photosynthesis (g C/m ² -day)	Av. total night respiration (g C/m ² -day)	P/R ratio
<i>Anthocephalus cadamba</i>	Valley	0.29	0.049	0.29	0.203	0.106	1.9
<i>Cecropia peltata</i>	Valley	0.30	0.020	0.30	0.223	0.047	4.7
	Forest	0.14	0.04	0.02*	0.15	0.770	0.170	4.5
<i>Sloanea berteriana</i>	Valley	0.05	0.01†	0.03	0.049	0.013	3.7
	Forest, open system	0.005	0.039	0.060	3.6
<i>Dacryodes excelsa</i>	Forest, closed system	0.14	0.03	0.03*	0.07	0.460	0.450	1.01
	Valley	0.06†	0.03	0.033	0.007	4.7
	Forest, open system	0.013	0.031	0.078	0.3
Forest, closed system	0.06	0.05	0.007*	0.005	0.175	0.210	0.79
Forest, closed system	0.063†

*Morning compensation point.

†Evening compensation point.

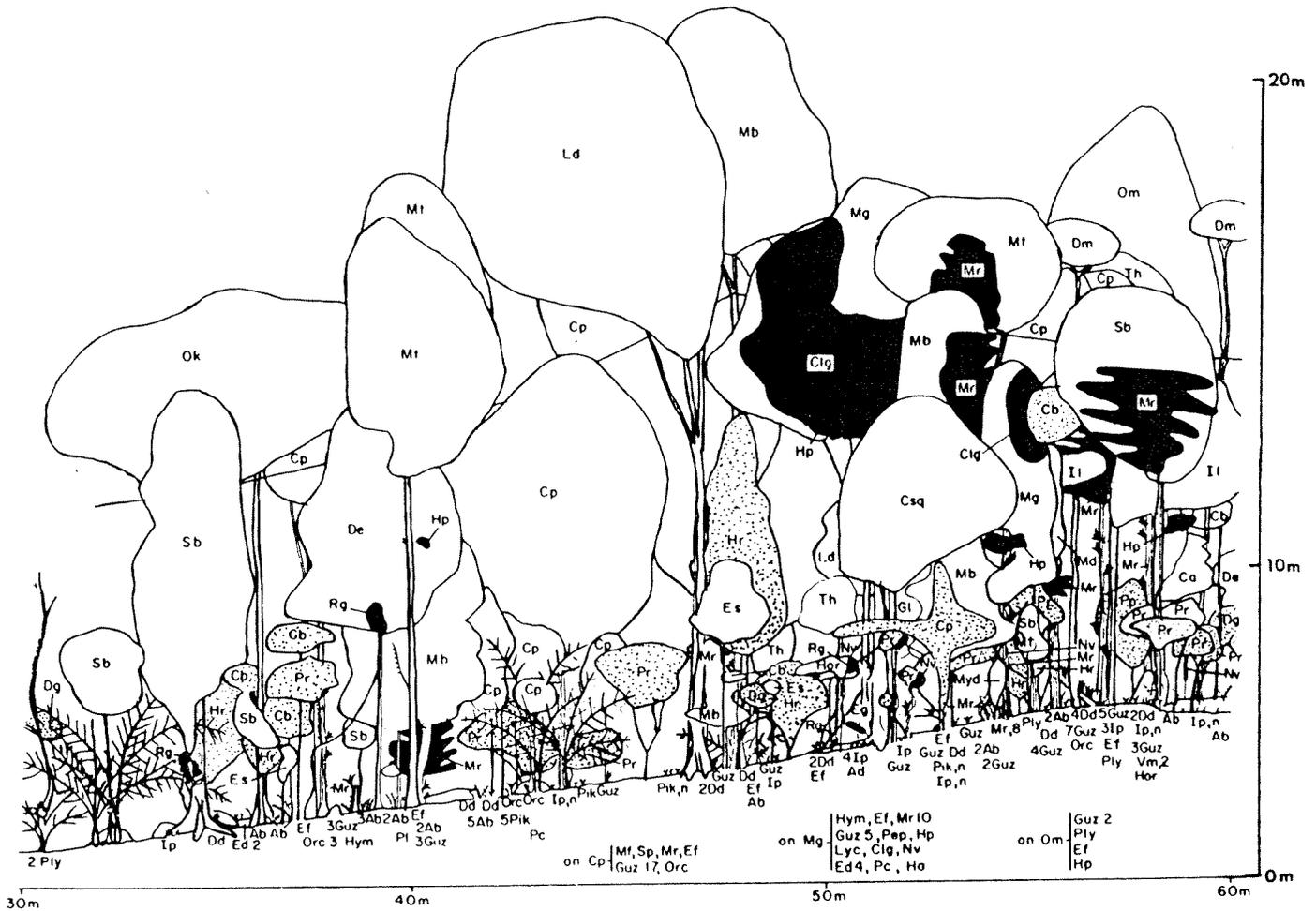


Figure 41.—Vertical profile of the tabonuco forest at El Verde (Smith 1970b). Profile includes all woody plants greater than 1.4 m tall extending horizontally from 30 m to 60 m in the radiation plot. Black crowns are climbers, small black plants are herbs and epiphytes, stippled crowns are understory, and clear crowns are canopy species. The symbols are the initials of the Latin names found in table 40.

density of epiphytes was $0.41/m^2$, a low value relative to that of the dwarf forest. The paucity of vegetation on the forest floor is evident from the low density of herbs, $1.44/m^2$ and seedlings, $4.16/m^2$. Over half of the herbaceous vegetation was composed of 2 species, *Ichnanthus pallens* and *Pilea krugii*. All species lists show the large number of species represented by only a few individuals.

Valuable for future comparative studies are the detailed quantitative descriptions of the vegetation structure and species composition of the study sites, including mapping of individual trees and vertical structural profiles (fig. 41).

The tabonuco forest of the Luquillo Experimental Forest was also compared to virgin tabonuco forests of Dominica, often used as an original model for those of Puerto Rico (Perez 1970; Soriano-Ressy et al. 1970). The dominant species in both was tabonuco, but the largest trees in Puerto Rico were shorter and had less basal area than in Dominica (table 41). Basal area in the El Verde tabonuco forest, measured

in many areas, ranged from 28–50 m^2/ha (Odum 1970b) but basal area in tabonuco forests of Dominica ranged from 90–131 m^2/ha .

Vertical Microclimatic Profiles.—Turbulence, typical of mountains, results in vertical differences which may not be as distinct in the tabonuco forest as those of other tropical rain forests. In general, however, temperature, evaporative power, throughfall, and wind velocity decrease and relative humidity and CO_2 concentration increase toward the forest floor (fig. 42). Except for occasional sunflecks, insolation reaching the forest floor may be as little as 3 to 8% of that received above the canopy and, similar to temperate forests, far-red light predominates inside the forest (table 42). Sunflecks, bright spots of light passing through gaps in the canopy, were shown to increase net photosynthesis and seedling growth (Lugo 1970) and may also play an important role in evapotranspiration and germination (Odum et al. 1970).

Leaf Area Index.—Results of several methods used

Table 37.—Number of trees by size class in 4 ha of virgin tabonuco forest (Wadsworth 1951)

Species	Number of trees by dbh (cm)				
	10-15	20-25	30-35	40+	Total
<i>Dacryodes excelsa</i> Vahl.	116	53	76	63	308
<i>Euterpe globosa</i> Gaertn.*	991	25	1,016
<i>Cecropia peltata</i> L.	214	80	37	6	337
<i>Micropholis garcinifolia</i> Pierre	74	60	43	4	181
<i>Sloanea berteriana</i> Choisy	87	16	21	8	132
<i>Cyrilla racemiflora</i> L.	4	9	11	16	40
<i>Magnolia splendens</i> Urban	6	5	7	15	33
<i>Inga laurina</i> (Sw.) Willd.	39	20	11	2	72
<i>Inga vera</i> Willd.	23	18	12	2	55
<i>Didymopanax morototoni</i> (Aubl.) Dcne.	33	24	10	1	68
<i>Calycogonium squamulosum</i> Cogn.	62	26	8	96
<i>Croton poecilanthus</i> Urban	83	14	4	101
<i>Alchornea latifolia</i> Sw.	31	10	5	3	49
<i>Alchorneopsis portoricensis</i> Urban	22	9	11	42
<i>Micropholis chrysophylloides</i> Pierre	12	8	4	1	25
<i>Ocotea spathulata</i> Mez	14	8	6	28
<i>Manilkara nitida</i> (Sesse & Moc.) Dubard	35	5	1	1	42
<i>Guarea trichiliodes</i> L.	20	7	2	1	30
<i>Eugenia stahlii</i> (Liaersk) Krug & Urban	11	12	4	27
<i>Matayba domingensis</i> (DC.) Radlk.	26	8	2	36
<i>Sapium laurocerasus</i> Desf.	26	10	1	37
<i>Homalium racemosum</i> Jacq.	5	1	2	8
<i>Ormosia krugii</i> Urban	6	2	1	9
<i>Meliosma herberti</i> Rolfe	7	6	2	15
<i>Buchenavia capitata</i> (Vahl.) Eichl.	2	2	1	1	6
<i>Hufelandia pendula</i> (Sw.) Nees	2	1	1	1	5
<i>Linociera domingensis</i> (Lam.) Knobl.	9	6	1	16
<i>Andira jamaicensis</i> (W. Wright) Urban	9	2	1	12
<i>Tabebuia pallida</i> Miers	17	1	18
<i>Cordia borinquensis</i> Urban	19	19
<i>Cithreoxylum fruticosum</i> L.	9	2	11
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	6	3	9
<i>Drypetes glauca</i> Vahl.	9	1	10
<i>Ocotea moschata</i> (Pavon.) Mez.	4	4
31 other species	193	35	12	3	243
Totals	2,226	487	296	131	3,140

*Now referred to as *Prestoea montana* (Sierra palm).

to estimate leaf area index of the tabonuco forest are presented in table 43. Values in undisturbed forest range from 5.24 to 7.3 with a mean of 6.3. Disturbed areas of the forest quickly recovered their LAI, e.g. after one year of cutting or irradiation, LAI was more than 50% of the undisturbed forest (table 43).

Chlorophyll a.—Chlorophyll *a* content of ecosystems is an important parameter with respect to the interpretation of productivity and photosynthetic structure. Mean chlorophyll *a* content of the tabonuco forest was 2.46 g/m² ground surface (Odum and CINTRÓN 1970), which falls in the upper range of values reported for other forest ecosystems. Mean chlorophyll *a* content of individual species ranged from approximately 0.3–0.4 g/m² leaf surface (fig. 43). Shade leaves had more chlorophyll *a* content than sun leaves (fig. 43). The higher chlorophyll *a* con-

tent of shade leaves suggests an adaptation to reduce light intensities inside the forest. Old leaves, generally located in the shade, also had higher chlorophyll *a* content than new leaves (fig. 43). In general, climax species had higher chlorophyll *a* than successional species. Odum et al. (1970) found that chlorophyll *a* varied seasonally (table 44). In January, when solar insolation was low, mean chlorophyll *a* content of tabonuco was approximately 20% higher than in May when solar radiation was higher. However, this trend was unsupported by data for the three species, including tabonuco, shown in figure 44, which show no seasonal trend in chlorophyll *a* content.

Biomass.—Measurements of biomass are useful in the comparison of different systems. A synthesis of all available data concerning the biomass of principal

Table 38.—Ranking of tree species in the tabonuco forest by density, basal-area dominance, and volume (Briscoe and Wadsworth 1970)

Scientific name	Density	Basal-area dominance†	Volume†
<i>Dacryodes excelsa</i>	1	1	1
<i>Euterpe globosa</i> *	2	2	2
<i>Sloanea berteriana</i>	3	9	9
<i>Cordia borinquensis</i>	4	26	26
<i>Manilkara bidentata</i>	5	10	10
<i>Didymopanax morototoni</i>	6	7	8
<i>Cecropia peltata</i>	7	5	5
<i>Micropholis garciniaefolia</i>	8	3	3
<i>Calycogonium squamulosum</i>	9	15	14
<i>Quararibaea turbinata</i>	10	23	23
<i>Miconia prasina</i>	11	27	27
<i>Ormosia krugii</i>	12	4	4
<i>Psychotria grandis</i>	13	30	30
<i>Ocotea moschata</i>	14	13	13
<i>Matayba domingensis</i>	15	12	12
<i>Micropholis chrysophylloides</i>	16	6	6
<i>Croton poecilanthus</i>	17	20	21
<i>Hirtella triandra</i>	18	24	24
<i>Tetragastris balsamifera</i>	19	11	11
<i>Alchornea latifolia</i>	20	19	19
<i>Meliosma herbertii</i>	21	18	18
<i>Alchorneopsis portoricensis</i>	22	22	22
<i>Inga vera</i>	23	16	17
<i>Guarea guidonia</i>	24	21	20
<i>Tabebuia heterophylla</i>	25	14	15
<i>Drypetes galuca</i>	26	28	28
<i>Buchenavia capitata</i>	27	8	7
<i>Andira inermis</i>	28	25	25
<i>Cordia sulcata</i>	29	29	29
<i>Inga laurina</i>	30	17	16

†Comparative rank within the 30 species of highest density only. Other species exceed ranks 9 and lower by basal area rank 7 and lower by volume.

**Prestoea montana*.

compartments in the tabonuco forest is shown in figure 45. At the El Verde site, 64% of total biomass (42.4 kg/m²) was attributed to above and below ground plant material; biomass of soil organic matter accounted for 34% of the total. Total plant biomass of 27.2 kg/m² was divided up as follows: 3% as leaves, 27% as roots, and 70% as bole and branch wood. The biomass contained in the woody portion is similar to or slightly less than that of other tropical forests, whereas root biomass appears to be higher than that of other tropical forests. Total above ground biomass of the forest at El Verde is within the range of 20–37 kg/m² reported for other tropical mature forests (Lugo et al. 1974).

Primary Productivity and Metabolism.—Gross primary productivity of the tabonuco forest at El Verde was measured by means of CO₂ infrared analysis on seedlings, sun and shade leaves of mature trees,

and an entire forest prism. Gross photosynthesis rates measured on individual leaves and extrapolated to the whole forest, using the leaf area index, resulted in estimates of gross primary productivity for the forest (30.4–39.0 g dry wt/m²·day) that were similar to the results obtained by enclosing an entire forest prism (32.8 g dry wt/m²·day; table 45). Mean efficiency of gross primary productivity, based on total solar insolation, was approximately 3%. The tabonuco forest showed more gross primary productivity than most other natural ecosystems. Its efficiency of light utilization, however, was similar to other natural and agricultural systems.

Gross primary productivity may be allocated to net growth and respiration. Total net biomass production at El Verde was estimated from the balance of wood growth (0.67 g dry wt/m²·day), tree loss due to mortality and decomposition (0.46 g dry wt/m²·

day), and leaf and fruit fall (1.52 g dry wt/m²·day) to be 1.74 g dry wt/m²·day or 5% of gross primary productivity (table 45).

The remainder of gross primary productivity was utilized by various components in respiratory processes (table 45). Total respiration of the forest ecosystem was estimated to be 33.4 g dry wt/m²·day and was approximately equal to total gross primary productivity. Respiration was highest in roots (51%), leaves (28%), and woody tissues (7%). Animal biomass was an insignificant fraction of the total biomass, but respiration of the animal compartment accounted for 3% of total respiration; soil microbial consumers accounted for 5% of total respiration.

In general, respiration (R) was greater than gross photosynthesis (P) in shade leaves (table 46). This was particularly pronounced in shade leaves of mature trees, e.g., *Sloanea* shade leaves had P/R ratios of 0.01–0.39 and sun leaves of *Manilkara* had P/R ratios of 0.3–2.7 (table 46). The energy to drive the forest system was derived primarily from some excess net photosynthate of the canopy leaves just below the upper layer. An alternative role for the leaves in the upper layer may be evapotranspiration, and for the epiphytic encrusted shade leaves it may be mineral cycling (Odum et al. 1970).

Energy Budget.—Daily average inflow of solar insolation was estimated to be 3,830 kcal/m²·day with a daily range of 1,000–8,000 kcal/m²·day. Auxiliary inputs which also drive the system include energy in mineral and nutrient sources, the flow of dry air, and energy in raindrops (fig. 46). Although relative to solar energy inputs these auxiliary inputs have low heat content, their energy amplifying effect in the forest is probably very high.

Downward flow of fixed energy to respiration sites is shown in fig. 47. Of total input of 3,830 kcal/m²·day from the sun, only 131 kcal/m²·day are fixed in gross photosynthesis. Of this, 38 kcal/m²·day is respired by the leaves themselves. Sixty-six percent of gross photosynthesis is transported downward by the phloem to various sites of respiration, and then to animals via grazing or decomposition. Animals receive energy primarily from the litter (66%) and grazing (30%), but a small portion may also be derived from vascular flow. Microbes receive approximately one-half of their energy source directly from the litter and the remainder following incorporation into the soil organic matter. Export of energy from the system via runoff waters was low, only 0.23 kcal/m²·day.

Table 39.—Importance values of principal trees in 4 ha of tabonuco and colorado forest (Wadsworth, R. K. 1970)

Species*	Tabonuco	Colorado	Ratio
Indicators of Tabonuco type			
<i>Alchorneopsis portoricensis</i> Urban	53	3	17.7
<i>Inga vera</i> Willd.	46	3	15.3
<i>Dacryodes excelsa</i> Vahl	130	30	4.3
<i>Sloanea berteriana</i> Choisy	89	34	2.6
<i>Inga laurina</i> (Sw.) Willd.	74	26	2.6
<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	72	33	2.2
<i>Alchornea latifolia</i> Sw.	55	28	2.0
<i>Sapium laurocerasus</i> Desf.	42	21	2.0
<i>Cecropia peltata</i> L.	109	58	1.9
<i>Miconia tetrandra</i> (Sw.) D. Don	85	55	1.5
Indicator of both types			
<i>Euterpe globosa</i> Gaertn.**	132	131	1.0
Indicators of Colorado type			
<i>Magnolia splendens</i> Urban	47	57	0.8
<i>Matayba domingensis</i> (DC) Radlk.	34	41	0.8
<i>Micropholis garciniaefolia</i> Pierre	83	121	0.69
<i>Calycogonium squamulosum</i> Cogn.	72	108	0.67
<i>Ocotea moschata</i> (Meisn.) Met.	47	83	0.53
<i>Croton poecilanthus</i> Urban	40	93	0.4
<i>Cyrilla racemiflora</i> L.	34	124	0.27
<i>Micropholis chrysophylloides</i> Pierre	12	86	0.14

*Species are arranged in order of the ratio of the importance values in Tabonuco forest to importance values in Colorado forest. (Data were taken from Tropical Forest Experiment Station, 1951).

***Prestoea montana*

Table 40.—Species composition of the tabonuco forest at El Verde arranged by synusiae and by density (Smith 1970b)

Name	Relative density %*	Name	Relative density %*
CANOPY TREES —Species with dbh > 10 cm		Total absolute density: 0.224 tree/m ²	
Total area sampled: 1.57 ha		Total density including all plants from 1.4 m tall to 10 cm dbh: 0.725 tree/m ²	
Total absolute density: 0.087 tree/m ²			
<i>Dacryodes excelsa</i> Vahl	18.2	<i>Palicourea riparia</i> Benth.	41.5
<i>Euterpe globosa</i> Gaertn.	11.4	<i>Drypetes glauca</i> Vahl	19.4
<i>Croton poecilanthus</i> Urban	9.5	<i>Cordia borinquensis</i> Urban	10.7
<i>Sloanea berteriana</i> Choisy	8.1	<i>Hirtella rugosa</i> Pers.	7.4
<i>Manilkara bidentata</i> (A. DC.) Cher.	6.4	<i>Psychotria berteriana</i> DC.	3.8
<i>Miconia tetrandra</i> (Sw.) D. Don	5.5	<i>Myrcia leptoclada</i> DC.	3.6
<i>Cecropia peltata</i> L.	4.6	<i>Trichilia pallida</i> Sw.	3.3
<i>Ormosia krugii</i> Urban	3.1	<i>Ixora ferrea</i> (Jacq.) Benth.	2.9
<i>Matayba domingensis</i> (DC.) Radk.	3.0	<i>Lasianthus lanceolatus</i> (Griseb.) Urban	1.9
<i>Inga jagifolia</i> (L.) Willd.	2.7	<i>Cassipourea guianensis</i> Aubl.	1.5
<i>Linociera domingensis</i> (Lam.) Knobl.	2.0	<i>Myrcia splendens</i> (Sw.) DC.	0.9
<i>Alchornea latifolia</i> Sw.	1.9	<i>Guarea ramiflora</i> Vent.	0.7
<i>Alchorneopsis portoricensis</i> Urban	1.8	<i>Comocladia glabra</i> (Schultes) Spreng.	0.7
<i>Sapium laurocerasus</i> Desf.	1.7	<i>Ocotea portoricensis</i> (Mez)	0.5
<i>Tabebuia pallida</i> Miers	1.7	<i>Daphnopsis philippiana</i> Krug & Urban	0.3
<i>Buchenavia capitata</i> (Vahl) Eichl.	1.7	<i>Ardisia glauciflora</i> Urban	0.3
<i>Micropholis garciniaefolia</i> Pierre	1.6	<i>Wallenia pendula</i> (Urban) Mez	0.3
<i>Ocotea leucoxydon</i> (Sw.) Mez	1.1	<i>Guatteria caribaea</i> Urban	0.3
<i>Calycogonium squamulosum</i> Cogn.	1.1	<i>Piper treleaseanum</i> Britton & Wilson	0.3
<i>Guarea trichilioides</i> L.	1.1	<i>Piper blattarum</i> Spreng.	0.2
<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	1.0	<i>Chlorophora tinctoria</i> (L.) Gaud.	0.1
<i>Inga vera</i> Willd.	1.0	<i>Ditta myricoides</i> Griseb.	0.1
<i>Eugenia stahlii</i> (Kiaersk.) Krug & Urban	0.9	<i>Samyda spinulosa</i> Vent.	0.1
<i>Cyrilla racemiflora</i> L.	0.9	<i>Urera baccifera</i> (L.) Gaud	
<i>Guettarda laevis</i> Urban	0.9	<i>Piper aduncum</i> L.	
<i>Ocotea spathulata</i> Mez	0.7	<i>Palicourea crocea</i> (Sw.) R. & S.	
<i>Casearia sylvestris</i> Sw.	0.6	<i>Psychotria maleolens</i> Urban	
<i>Homalium racemosum</i> Jacq.	0.5	<i>P. patens</i> Sw.	
<i>Casearia arborea</i> (L.C. Rich.) Urban	0.5	<i>P. brachiata</i> Sw.	
<i>Cordia sulcata</i> DC.	0.5	<i>P. uliginosa</i> Sw.	
<i>Ocotea moschata</i> (Meisn.) Mez	0.5	<i>Rondeletia portoricensis</i> Krug & Urban	
<i>Casearia bicolor</i> Urban	0.5	<i>Brunfelsia portoricensis</i> Krug & Urban	
<i>Byrsonima coriacea</i> (Sw.) DC.	0.5	<i>Hedyosmum arborescens</i> Sw.	
<i>Tetragastri balsamifera</i> (Sw.) Kuntze	0.4	<i>Mecranium amygdalinum</i> (Desr.) C. Wright	
<i>Miconia prasina</i> (Sw.) DC.	0.3	<i>Laplacea portoricensis</i> (Krug & Urban) Dyer	
<i>Symplocos</i> sp.	0.3	<i>Oxandra laurifolia</i> (Sw.) A. Rich	
<i>Magnolia splendens</i> Urban	0.3	<i>Cestrum macrophyllum</i> Vent.	
<i>Meliosma herbertii</i> Rolfe	0.2	<i>Rheedia acuminata</i> (Spreng.) Planch. & Tr.	
<i>Henrietella fascicularis</i> (Sw.) C. Wright	0.2	<i>Malphigia fucata</i> Ker.	
<i>Myrcia deflexa</i> (Poir.) DC	0.1	<i>Myrcia berberis</i> DC.	
<i>Eugenia jambos</i> (L.) Millsp.		<i>Coccoloba pyrifolia</i> Desf.	
<i>Roystonea borinquena</i> O. F. Cook		<i>Miconia racemosa</i> (Aubl.) DC	
<i>Beilschmiedia pendula</i> (Sw.) Benth. & Hook. f.		<i>Miconia sintenisii</i> Cogn.	
<i>Cyathea arborea</i> (L.) J. E. Smith		<i>Miconia guianensis</i> (DC) Cogn.	
<i>Antirhea coriacea</i> (Vahl) Urban		<i>Maytenus</i> sp.	
<i>Micropholis chrysophylloides</i> Pierre		<i>Piptocarpha tetrantha</i> Urban	
<i>Citharexylum caudatum</i> L.		<i>Tabernaemontana oppositifolia</i> (Spreng.) Urban	
<i>Pisonia subcordata</i> Sw.			
<i>Byrsonima wadsworthii</i> Little			
<i>Haenianthus salicifolius</i> var. <i>obovatus</i> Knobl.			
<i>Andira inermis</i> (W. Wright) H. B. K.			
<i>Coccoloba swartzii</i> Meisn.			
<i>Ilex sideroxyloides</i> (Sw.) Griseb.			
<i>Nectandra sintenisii</i> Mez			
UNDERSTORY TREES —Species that flower under the main canopy and low shrubs of secondary forests		CLIMBERS —Individuals that had leaves in the main canopy	
Total area sampled: 0.28 ha		Total area sampled: 0.28 ha	
		Total absolute density: 0.133 plant/m ²	
		<i>Rourea glabra</i> Griseb.	28.4
		<i>Philodendron krebsii</i> Schott	18.0
		<i>Marcgravia rectiflora</i> Tr.	14.0
		<i>Heteropteris laurifolia</i> (L.) Juss.	13.7
		<i>Schlegelia brachyantha</i> Griseb.	4.9
		<i>Neorudolphia volubilis</i> (Willd.) Britton	4.0
		<i>Securidaca virgata</i> Sw.	4.0
		<i>Paullinia</i> sp.	3.4

Table 41.—Basal area by height class in tabonuco forest of Dominica and Puerto Rico (Soriano-Ressy et al. 1970)

Class	Height Range (cm)	Dominica			Puerto Rico			
		Palmist Ridge	Dleau Gommier	Pagayer	El Verde South Control Center	El Verde Radiation Center	Sabana	Sabana
4	70 to 180	0.013	0.004	0.087	0.012	0.004	0.004	0.001
5	180 to 500	0.003	0.113	0.007	0.017	0.021	0.011	0.011
6	500 to 1300	0.045	0.023	0.072	0.106	0.124	0.044	0.073
7	1300 to 3500	0.489	0.242	1.065	0.238	0.264	0.217	0.219
8	3500 and over	0.759	0.523
Totals		1.309	0.905	1.231	0.373	0.413	0.276	0.304

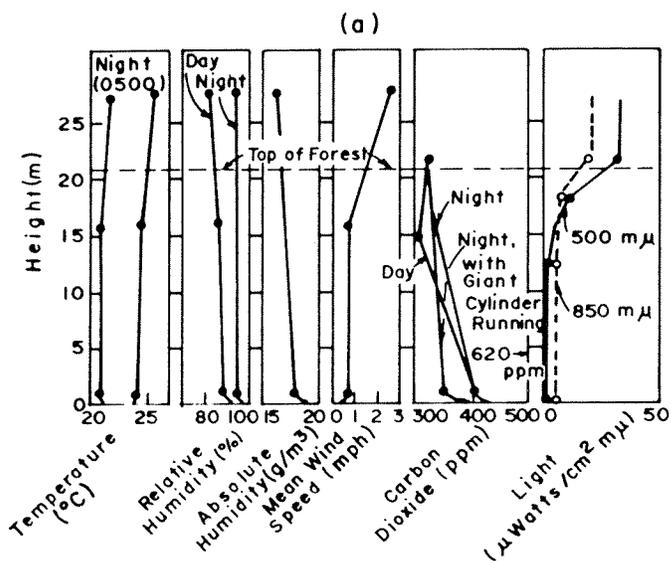


Table 42.—Light quality and intensity in the tabonuco forest at El Verde (Johnson and Atwood 1970)

		10 ⁻⁴ calories/cm ² -min	
		Apr. 1966	Mar. 1967
Direct sunlight at top of the canopy	400-700 mμ	2441.1	1756.6
	700-1000 mμ	1383.8	793.6
Total		3824.9	2550.2
Percent infrared		36	31
Shade light on the forest floor	400-700 mμ	9.4	12.1
	700-1000 mμ	48.2	17.8
Total		57.6	29.9
Percent infrared		84	60

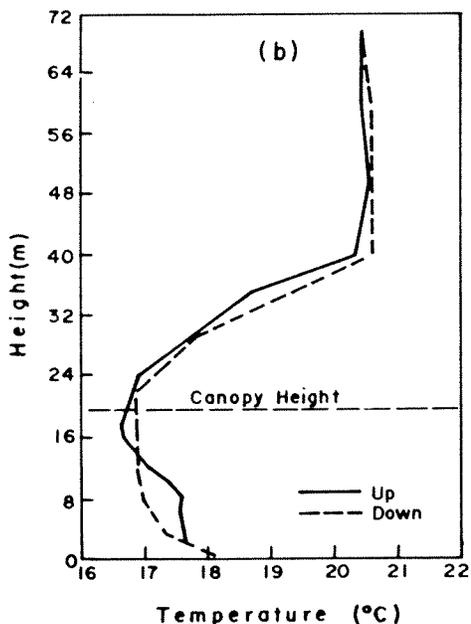


Table 43.—Leaf-area index of tabonuco forest as estimated by several methods (Odum 1970b)

Procedures	Leaf area (one side)
	Area of ground
Ten prisms (Odum, Copeland, and Brown, 1963)	6.4
Sabana biomass plot (Odum, 1962)	7.3
Giant cylinder, plumb line	5.24
Plumb line*	5.6
Three 183 m transects using correlation of spectral ratio to biomass*	6.6
Radiation Center	
One year after irradiation*	3.16
Three years after irradiation*	5.51
North Cut Center	
One year after cutting*	4.03
Three years after cutting*	4.45

*Jordan (1968).

Figure 42.—(a) Vertical gradient in microclimate in the tabonuco forest at El Verde. (b) Single day of record of temperature vs. height in the tabonuco forest at El Verde (Odum et al 1970c).

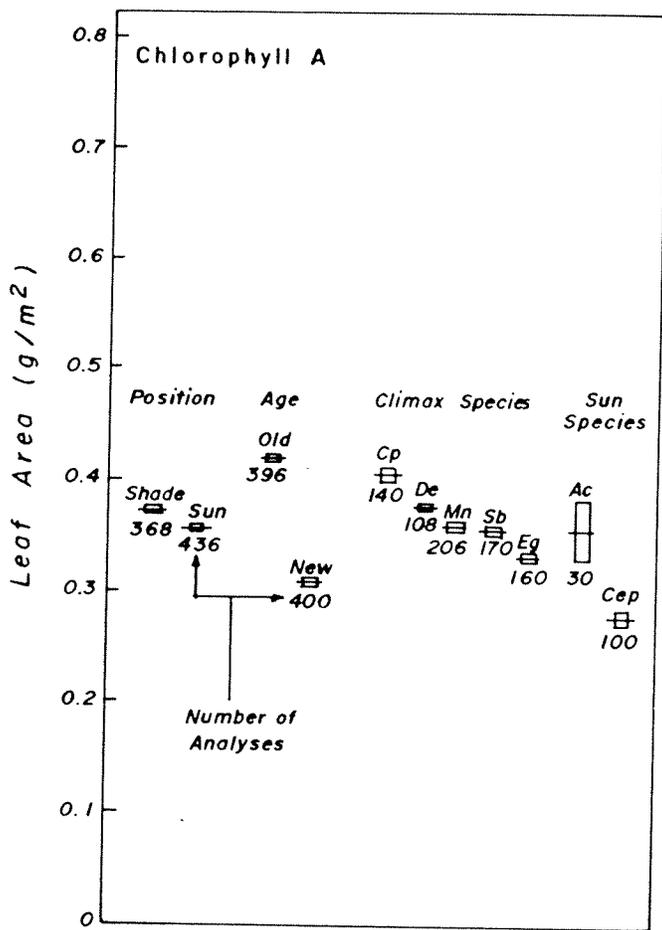


Figure 43.—Patterns of chlorophyll a distribution in leaves of the tabonuco forest at El Verde by sun and shade, age, and species. Cp = Croton peocilanthus; De = Dacryodes excelsa; Mn = Manilkara bidentata; Sb = Sloanea berteriana; Eg = Euterpe globosa; Ac = Anthocephalus cadamba; Cep = Cecropia peltata (Odum and Cintrón 1970). Horizontal lines represent the mean and vertical bar the standard error.

Turnover times (estimated from fig. 47) are fastest in fruit (5 days), small root (43.3 days), litter (170 days), and leaf (619 days) compartments. Slowest turnover times are in bole wood (6,131 days) and soil organic matter (9,350 days) compartments.

Evapotranspiration.—Total water loss from the tabonuco forest was divided almost equally between transpiration and the sum of evaporation, intercepted rain, and soil evaporation (table 47). However, evaporation of intercepted rain was a major pathway (2,650 g/m²·day) compared to evaporation from the soil surface (36 g/m²·day). Total evapotranspiration from the forest was equivalent to 4.8 mm/day, or an estimated 176 cm/yr. This represents approximately 50% of the annual rainfall. Items A–C in table 47 show the vertical distribution of transpiration rates. Top sun leaves had higher diurnal transpiration rates

Table 44.—Comparison of winter and summer chlorophyll a content of crown and shade leaves of tabonuco (*Dacryodes excelsa*) (Odum et al. 1970a)*

	January 1958			May 1959		
	N [†]	Mean (g/m ² leaf area)	SE [‡]	N [†]	Mean (g/m ² leaf area)	SE [‡]
Crown leaves						
12 to 14 m	9	0.403	0.0112	7	0.334	0.0865
Shades leaves						
2 to 12 m	19	0.434	0.0188	10	0.369	0.0134
Mean		0.424			0.355	

*Analysis of variance shows 5 to 10% level of significance between crown and shade levels and more than 1% significance between January and May samples taken.

[†]Number of measurements.

[‡]Standard error.

per leaf surface (465 g/m² leaf surface) than other canopy leaves (44–175 g/m² leaf surface). Evapotranspiration rates on dry days from the giant cylinder were lower than on moist days (c.f. item E and J in table 47), on dry days the leaves were dry thus there was no evaporation of intercepted rainfall.

Tree Growth.—Lateral stem growth was measured from 1963 to 1967 on 250 trees of five principal species (Murphy 1970). Absolute increases in basal area were approximately 2–12 times higher in trees in “full top light” than those in “some top light” positions (table 48). But percent increase was only approximately two times higher in “full top light” than in “some top light” positions. Tabonuco exhibited higher percent increase in the “some top light” position trees, but the actual basal area increase was higher in trees located in “full top light”. This apparent contradiction was due to the very large stem diameter of trees positioned in “full top light” (Murphy 1970).

No seasonality in mean monthly basal area increments for the five principal species was measured (fig. 48). Basal area increment did not appear to correlate with either rainfall (fig. 49a), or tree crown-top area (fig. 49b) for any of the five species. The data in figure 49b raises a question of whether maximum growth rate of a species occurs for those trees in the largest crown size class.

Mineral Cycling.—Mineral cycles were examined from measurements of biomass and chemical concentrations of various forest compartments and flows. Oven dry weight of leaves, branches, bole, fruit, flowers, roots, and epiphytes, as well as their element concentration, were determined for common species of the tabonuco forest. Leaf and leaf litter ash and soils were also analyzed for their elemental concentrations.

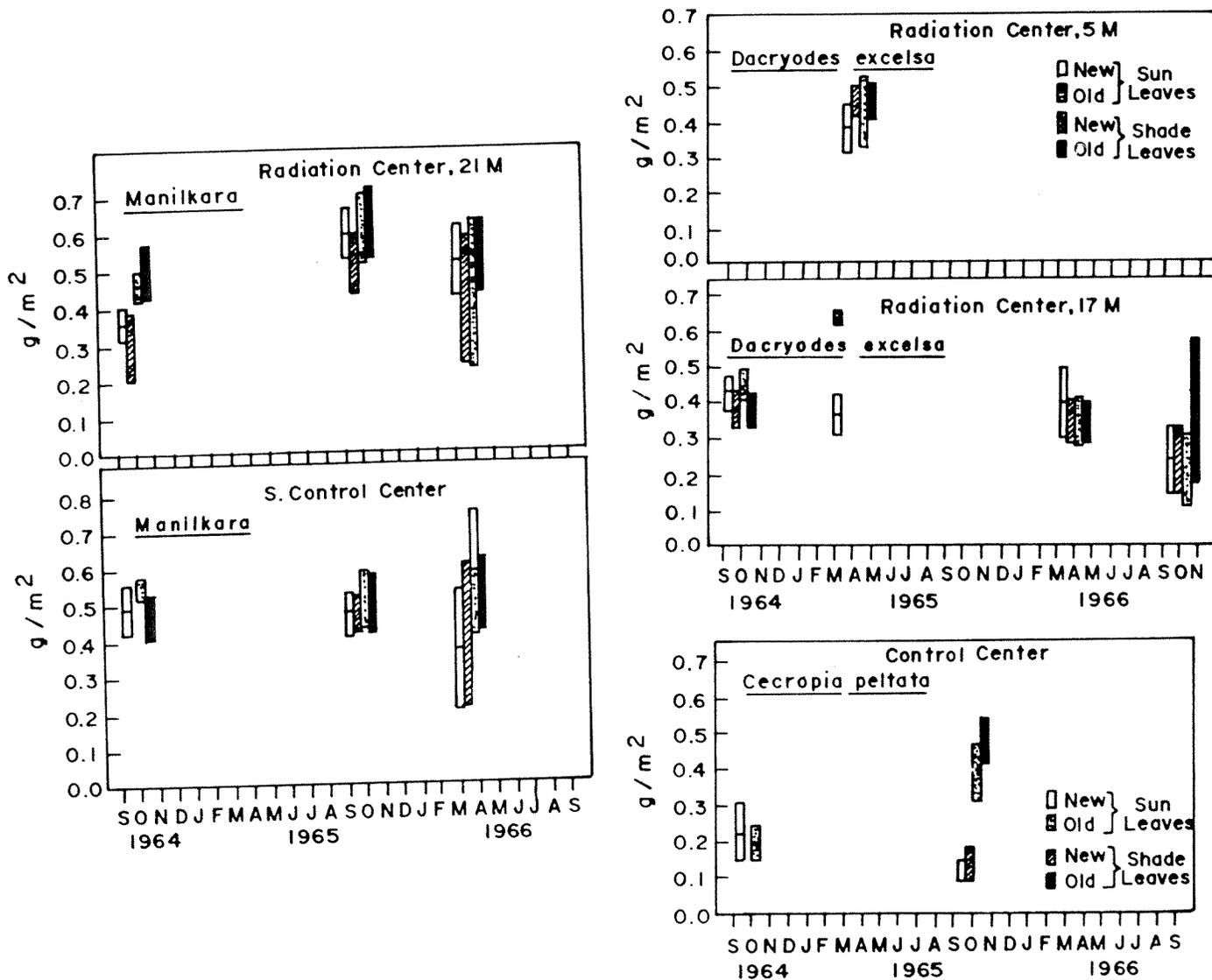


Figure 44.—Variation of chlorophyll a content with time in the tabonuco forest at El Verde (Odum and Cintrón 1970).

Mineral concentrations in various plant parts decreased in the following order: leaves, branches, small roots, large roots, butt roots, and boles (table 49). Concentrations of minerals in the litter were lower than in fresh leaves (with the exception of calcium which was higher).

Estimates of the magnitudes of storages and flows of a variety of minerals are shown in figure 50. Steady state conditions were assumed in estimating values for unknown pathways such as inputs from weathering and plant uptake. Input of minerals from rainfall was generally more important than from weathering. The exceptions to this general trend were magnesium and iron. Storage of minerals in plant biomass was generally higher than in soils and litter; from 55–84% of the total mineral storage was stored in plant tissues for all minerals except magnesium and iron, where 57% and 83%, respectively, of the total was stored in the soil and litter. Most minerals in

plants were stored in the woody material. For calcium, magnesium, manganese, and iron leaf fall was the major pathway of nutrient transfer to the soil, whereas for the other three minerals leaching by throughfall and stemflow was the major pathway. Output of minerals were either greater than or equal to inputs from rainfall.

Turnover times for the minerals shown in figure 50, range from less than 10 yr (sodium, potassium, and copper) to 10–20 yr (calcium and magnesium) and greater than 500 yr (manganese and iron). Essential elements had higher recycling rates and, therefore, a lower stability, indicating that recovery from perturbation would require a greater amount of time (Jordan et al. 1972).

Storages and flows (table 50 a and b) of stable isotopes of strontium (⁹⁰Sr) and manganese (⁵⁴Mn) were determined for the forest near El Verde and used to formulate a mathematical model of the dy-

namics of these two elements (Jordan et al. 1973). The model was then used to make predictions about the fate of radioactive analogs of these two isotopes which were deposited in the forest during the 1960's from radioactive fallout. Disappearance of the manganese isotope from all forest compartments was predicted to occur within less than 10 years because of the relatively short half-life of this isotope. Because ^{90}Sr has a much longer half-life than ^{54}Mn , it was predicted to remain in all compartments of the forests and undergo considerable recycling (fig. 51). The model predictions were tested in 1972 when samples of forest compartments were analyzed for ^{90}Sr (Jordan and Kline 1976). They found that ^{90}Sr values for leaves, wood, and soil approximated the predicted values but that the value for litter was higher than predicted (fig. 51). They suggested that the reason litter values were higher than predicted was due either to inaccuracy due to an inadequate sample size or that the litter compartment, being the smallest

compartment (lowest storage), shows the greatest relative change following changes in ecosystem inputs.

Nitrogen has long been considered to be a special problem in the tropics because of its low content in soils (Odum 1970a). Edmisten (1970e) found that major inputs of nitrogen occurred at leaf surfaces (60% of the total nitrogen input) and root nodules (26% of the total input) by nitrogen fixation; the remaining 14% of input was from rainfall (fig. 52). Epiphyllae fix nitrogen at the leaf surfaces and mycorrhizae fix nitrogen in the root nodules, (Edmisten and Kline 1968). Nitrogen transfer from leaf and fruit fall was as important as transfer from leaching and stemflow. Nitrogen losses by denitrification were 2.5 times higher than by runoff.

A summary of the flows and storages of hydrogen for the tabonuco forest are shown in figure 53. Inputs and outputs of hydrogen were measured by means of the giant cylinder (used to estimate metabolism of

Table 45.—Calculation of organic energy flows in the tabonuco forest at El Verde (Odum 1970b)

Description	Source	Flow rates		
		g dry mass/ m ² ·day	kcal/g	kcal/m ² · day
Incoming production, insolation				
Insolation				3830
Gross photosynthesis	Day net photosynthesis plus night respiration 32.8 g/m ² ·day	32.8	4	131.2
Net grain				
Wood deposition rate	0.67 g/m ² ·day	0.67	4	2.68
Wood loss rate	0.45 g/m ² ·day	0.45	4	1.76
Net wood deposition rate	Difference of previous two	0.22		0.72
Litter				
Roots to litter	Assumed same loss % as limbs	0.57	4	2.3
Leaf fall		1.38	4.2	5.80
Fruit fall		0.14	5	0.70
Brush fall		1.13	4	4.52
Log fall	Intermediate value	0.54	4	2.16
Organic drip	1.2 mg/l daily rain, 9.8 mm/day, throughfall, 55%	0.006	4	0.026
Metabolism				
Leaf respiration	4.7 g C/m ² ·day	9.4	4	38.2
Roots	8.56 g C/m ² ·day	17.1	4	68.4
Soil microbial consumers	Three methods; 2.1 minus earthworms (4.1 g × 92 mg O ₂ /g·day)	1.7	4	6.8
Fruit	0.31 mg C/g day, 2.4 g/m ²	0.015	5	0.075
Trunks	0.78 g C/m ² ·day	1.56	4	6.2
Limbs	0.40 g C/m ² ·day	0.80	4	3.2
Animals	12 g dry/m ² , 92 mg O ₂ /g dry·day	1.10	4	4.4
Litter		1.10	4	4.4
Log-stump decay	Metabolic method, old stumps From decay of fresh butts	0.15 0.44	4 4	0.60 1.76
Microbes to animals	10% of respiration			
Animals to microbes	10% of respiration			
Microbes to soil	10% of respiration			

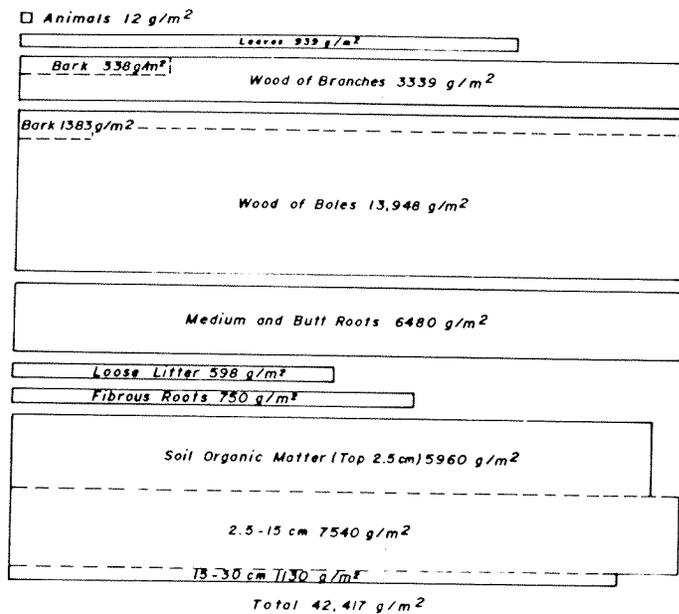


Figure 45.—Biomass (dry weight) in the tabonuco forest at El Verde (Odum 1970b).

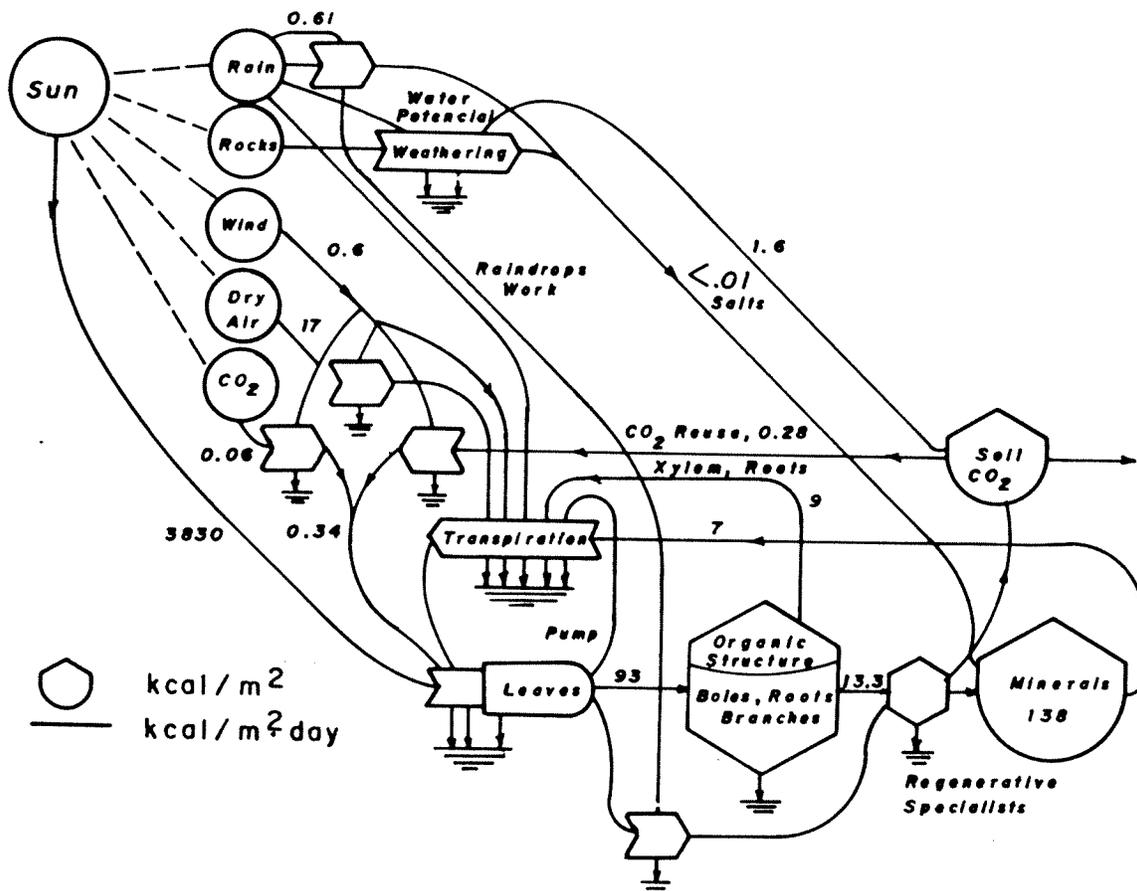


Figure 46.—Auxiliary energy inputs to the tabonuco forest system at El Verde (Odum 1970b).

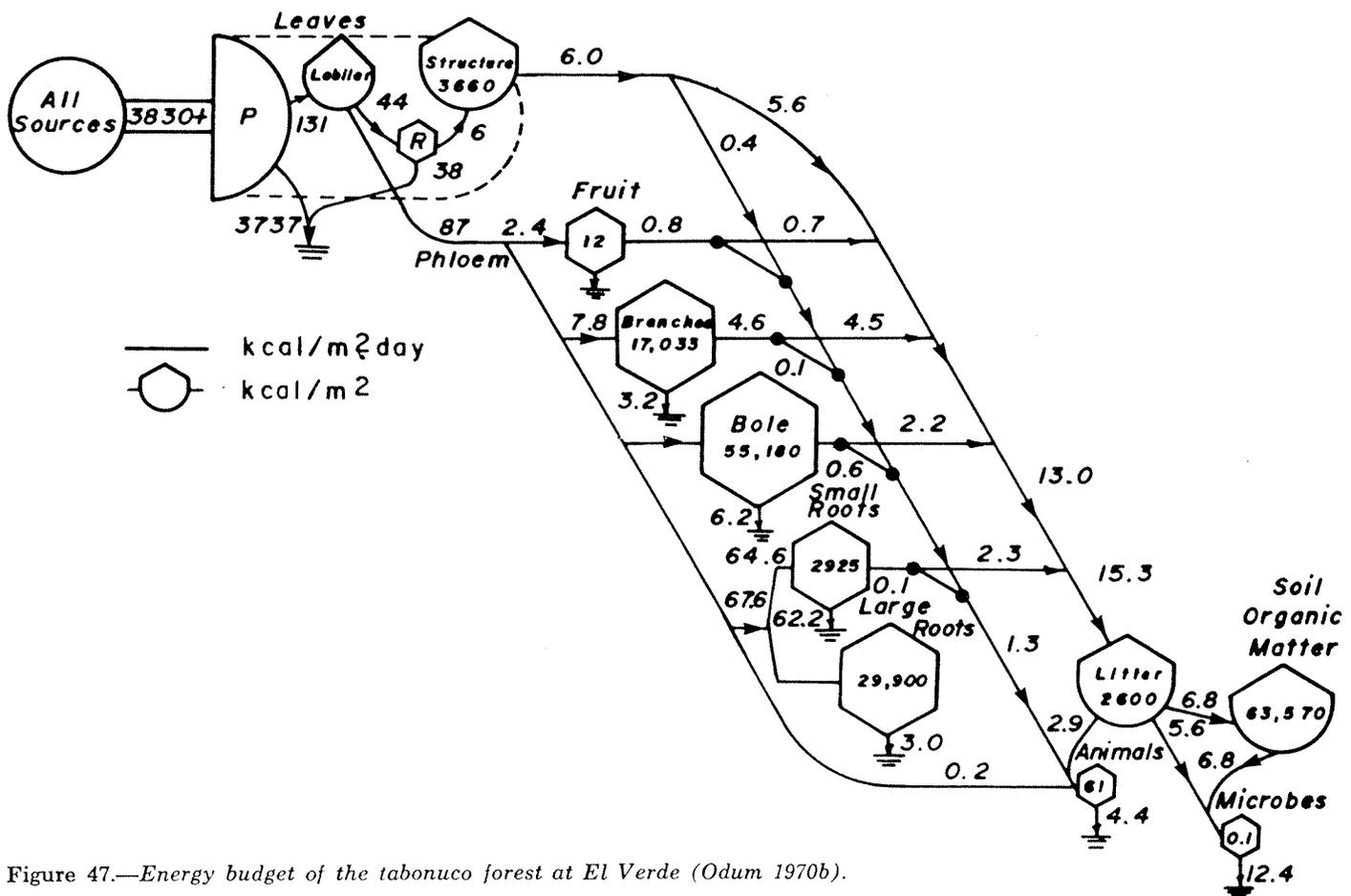


Figure 47.—Energy budget of the tabonuco forest at El Verde (Odum 1970b).

Table 47.—Evapotranspiration in the tabonuco forest at El Verde (Odum and Jordan 1970)

Calculation level	Number of leaves	Number of surfaces	Water loss rate per surface (gH ₂ O/m ² ·day)	Contribution to area of ground (g/m ² ·day)
A. Top sun leaf	1*	2	(<i>Dacryodes</i>)	929
B. Other canopy leaves	3.2*	6.4	(<i>Dacryodes</i> 350 and <i>Manilkara</i> series)	1120
C. Leaves in lower forest	1*	2	(<i>Dacryodes</i> 87 and <i>Sloanea</i> series)	87
D. Transpiration total for 5.2 leaves				2136
E. Giant cylinder on day with dry leaves, Feb. 24, 1966	5.2	11.4	Mean of Feb. 23 and Apr. 7	876
F. Evaporation of intercepted rain	5.2	10.4	(9.7 mm daily rain) (10 ³ g/m ² ·mm) (27.3%)	2650
G. Evaporation of intercepted rain from one leaf-side surface	0.5	1	2650 per 10.4 surfaces	255
H. Soil evaporation	1	1	Pan evaporation on forest floor	36
I. Total evapotranspiration	5.2	11.4	Sum of transpiration (D), soil evaporation (H), and evaporation of intercepted rain (F)	4822 (176 cm/yr)
J. Giant cylinder	5.2	11.4	Mean of 6 ordinary days	1261
K. Evapotranspiration lost from cylinder			By difference	3562
L. Evaporation caught in cylinder			Difference between ordinary day (J) and dry day (E)	385

*A leaf area is taken in units of leaf-area index; one leaf surface means both sides.

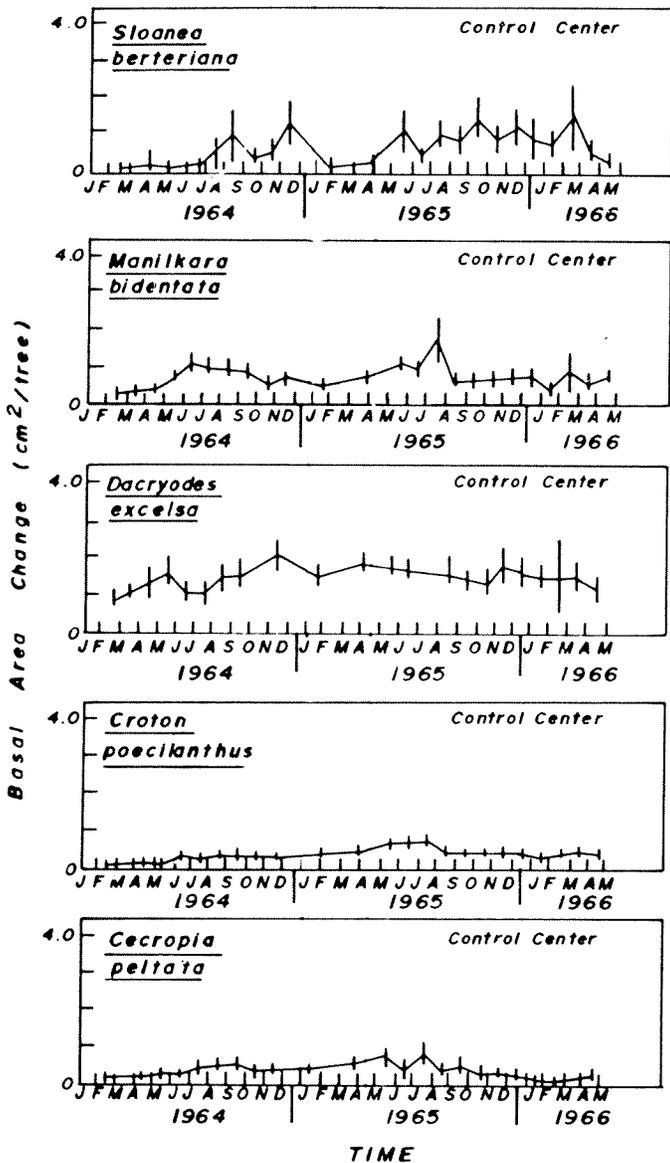


Figure 48.—Seasonality in tree growth in the tabonuco forest at El Verde (Murphy 1970).

Table 48.—Basal-area increase by crown position in the tabonuco forest (Murphy 1970)

Species	Basal-area increase			
	Percent increase		Absolute increase (cm ²)	
	Some top light	Full top light	Some top light	Full top light
<i>Cecropia peltata</i>	1.6	7.7
<i>Dacryodes excelsa</i>	3.6	2.5	6.8	23.2
<i>Manilkara bidentata</i>	2.5	4.9	4.6	17.5
<i>Sloanea berteriana</i>	0.9	1.7	1.7	20.9
<i>Croton poecilanthus</i>	1.4	3.0	3.7	9.6

the forest) and from tritium tracer studies. Storages of hydrogen in organic matter were estimated from the organic matter budgets by assuming that 7% of dry organic matter was hydrogen. Hydrogen inflow from rainfall (96%) and condensation (4%) was intercepted by the canopy (25%), and passed through as stemflow (18%) and throughfall (55%). Hydrogen losses from the system were equally divided between evaporation and transpiration and surface and subsurface runoff. Storages of hydrogen in the plant compartments as both water and organic forms was a small component of the total storage (19%). Approximately 55% of the hydrogen was stored in the soil profile. Compartments where hydrogen was stored as water had fast turnover rates (10 days). Where hydrogen was stored as organic matter, turnover times were longer. Woody tissue, the largest storage of organic matter had a turnover time of 9000 days.

The pattern of annual litterfall exhibited a distinct seasonal phenomenon (fig. 54). Peak leaf fall occurred from April to July, during the sunniest months when conditions for growth may be optimum, and least from December to March. Mean daily rate of litterfall was 1.4 g/m². On an annual basis mean litterfall rate was balanced by mean annual disappearance rate (table 51).

In a warm, high rainfall environment, such as the tabonuco forest special adaptations are necessary for retention of minerals and the maintenance of tight mineral cycles. Epiphytic growth may be particularly important in the retention of minerals. The "natural" tagging of vegetation with fallout radionuclides, ¹³⁷Cs, ⁵⁴Mn and ¹⁴⁴Ce, from atmospheric nuclear weapons tests facilitated the investigation of the role of these organisms in nutrient cycling. Plants with epiphytic growth had higher concentrations of these elements than plants without (Kline and Odum 1970). Retention of nuclides applied to leaf surfaces with epiphylls surpassed, by as much as twenty times, retention by leaves without (table 52). These minerals may subsequently be leached or taken up by foliar absorption.

Tracer studies with ⁸⁵Sr and ¹³⁴Cs indicated small nutrient loss via soil water (Jordan 1970b). Low activity of these tracers in soil water indicated retention by litter and upper layers of the soil (fig. 55). Failure of root uptake to account for high concentrations of fallout radionuclides in leaves described above was supported by additional tracer studies in understory plants (Kline and Mercado 1970). Within one year less than 1% of the ¹³⁴Cs, ⁵⁴Mn, and ⁸⁵Sr applied to four plots had been taken up by the vegetation and greater than 90% remained in the top 10 cm of soil.

Table 49.—Mineral content (percent of dry weight) of major compartments in the tabonuco forest (Odum 1970b)

Element	Perkins*		Ovington						Kline [†] leaves	Edmisten [§] and Perkins Soil exchangeable ions	Gruenwoldt [¶] Top soil
	Leaves	Litter	Leaves	Branches	Boles	Butt roots	Large roots	Small roots			
Nitrogen	1.606	0.619	0.336	0.340	0.336	0.683	0.46	2.12
Calcium	0.592	0.762	0.999	0.734	0.377	0.348	0.439	0.514	0.755	0.0450
Sodium	0.590	0.105	0.202	0.102	0.109	0.0288
Magnesium	0.264	0.167	0.366	0.152	0.085	0.098	0.123	0.173	0.279	0.0310
Potassium	0.186	0.0340	1.035	0.543	0.350	0.289	0.286	0.388	0.00338	0.0044
Phosphorus	0.022	0.0196	0.030	0.038	0.023	0.020	0.021	0.683	0.022
Manganese	0.0157	0.0092	0.027	0.0309
Strontium	0.0049
Iron	0.045	0.0039	0.0750
Zinc	0.00153	0.00125	0.000345
Copper	0.00083	0.00080	0.00134
Cobalt	0.00011

*Mean of five species given. Product of percentage of ash \times 5.8% ash of dry.

†Mean of nine species analyzed.

§Mean of top 25 cm in six pits, 12 analyses; nitrogen content.

¶Gruenwoldt (1962).

The unimportance of leaching as a mechanism of nutrient transfer was indicated by studies of fallout nuclides in the forest at El Verde. Little leaching occurred from seedlings, with the exception of *Pali-courea riparia* (Tukey 1970). Edmisten (1970a) reported that the presence of drip tips, a structural adaptation of some tropical rain forest species, resulted in reduced nutrient loss by leaves of *Ormosia krugii*. Bromeliads were found to be capable of absorbing and utilizing any of the nutrients leached from the vegetation above (Tukey 1970).

High population densities and number of species of microfungi suggest that decomposition processes start while the leaf is still attached to the tree (tables 53 and 54), particularly for the old leaves in the lower canopy.

Phenology.—Flowering, fruiting, and leaf fall of 73 species was followed from 1963 to 1967 (Estrada 1970). Although phenological patterns differed among species, the principal increase in fruit drop occurred during the winter months. Thus, seeds are available for germination during a time in spring when insolation, rainfall, and input of sea salts and nutrients increased. Although slight when compared to areas with a distinct dry season, seasonal pulses in germination, new leaf growth and leaf fall were noted and are illustrated in a calendar of events in figure 56. The slight seasonal pulse in leaf fall occurs not during the dry period, as most dry season forests, but rather in April and May. Rain, light, and new leaf growth also increase at this time (fig. 56).

Colorado Forest

Above the average cloud condensation level (600 m) is the colorado forest. It derives its name from the common palo colorado tree (*Cyrilla racemiflora*). The palo colorado has an unusual range. It is found in South and Central America and also in the U.S. from Florida to Texas and north to Virginia. In the latter region it is a small tree or shrub in swamps and on river banks (Little and Woodbury 1976). The Puerto Rican parrot, an endangered species, utilizes cavities in large palo colorado trees for nesting purposes. A decrease in the population of this species has been attributed in part to the scarcity of good nesting sites which has resulted from 1) the removal of large palo colorados for charcoal production, 2) the occupation by honeybees, and 3) by hurricanes in the early part of the century (Snyder 1978).

Physiognomy.—Accompanying an increase in soil moisture and organic matter content at higher elevation in the Luquillo Forest is a change in vegetation structure and species composition. Abundance and size class distribution of 27 arborescent species in 4 ha of virgin colorado forest is given in table 55. The average number of species per 0.4 ha, 23, is less than that of the tabonuco forest. The most numerous species are the sierra palm, *Micropholis garcinifolia* Pierre, *Calycogonium squamulosum* Cogn., and *Micropholis chrysophylloides* Pierre. The palo colorado ranks only sixth in abundance but it has the greatest number of individuals in the largest size class. Again, as in the tabonuco forest, the majority

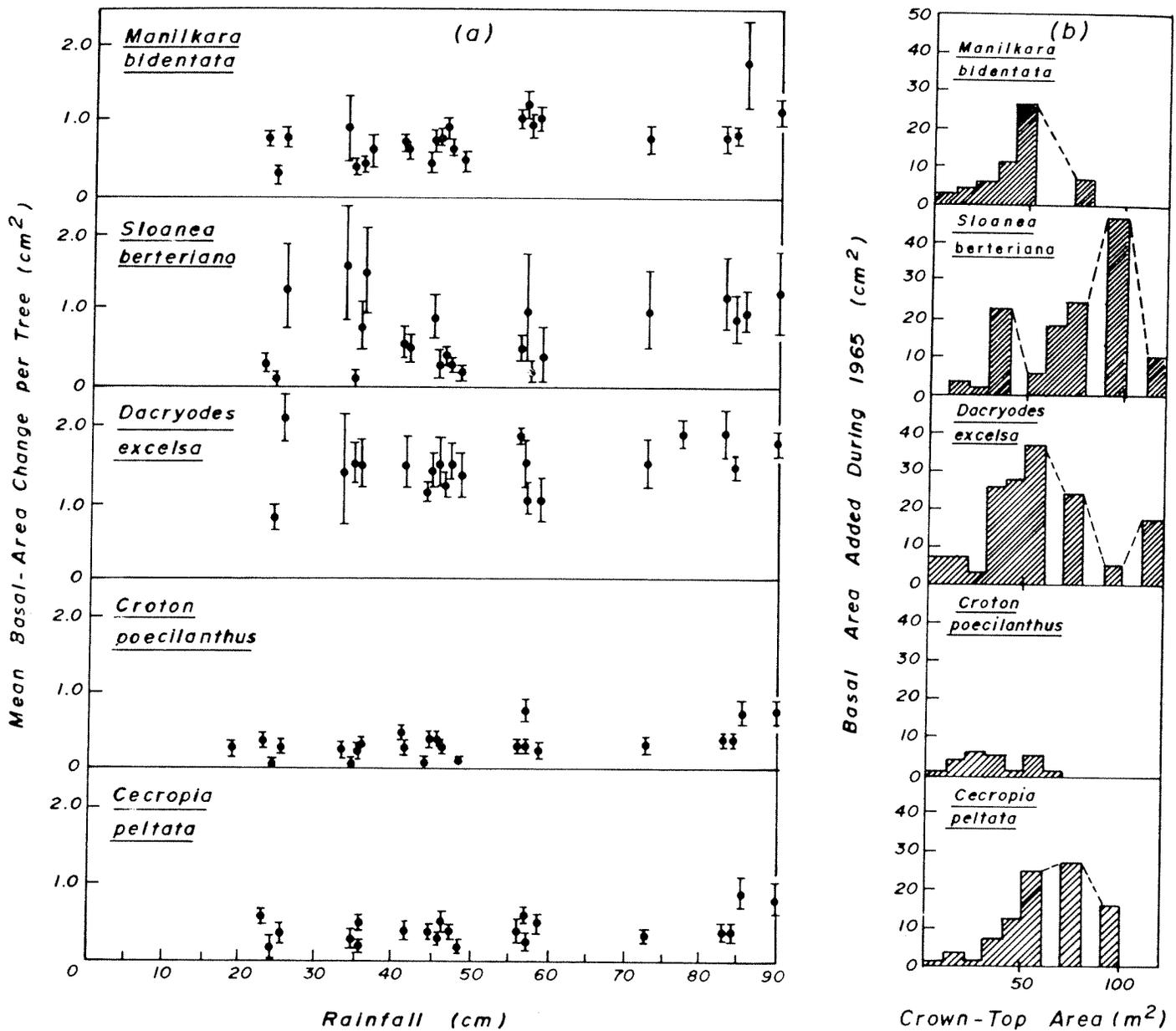


Figure 49.—Basal-area change as a function of (a) rainfall and (b) crown-top area in five species of the tabonuco forest at El Verde (Murphy 1970).

of palm stems are less than 15 cm in diameter.

Palo colorado, *Micropholis garcinifolia*, *M. chrysophylloides*, and *Ocotea spathulata* Mez. are more abundant in the colorado than any other forest type (Wadsworth 1951). Wadsworth (1951) lists four more species which, based on their importance values, may be considered indicator species (table 39).

Tree height in the colorado forest decreases to less than 15 m and their crowns begin lower and branch more profusely, lending a more crowded appearance to this forest than the tabonuco forest (table 56). The two tree strata are less readily distinguished than those of the tabonuco forest. Stem density is greater, but average diameter less. Leaves are gen-

erally smaller, thicker and more coriaceous. Buttress roots are less common, but vines and epiphytic growth more so. Soils are covered by thick surface networks of roots (see fig. 40) and herbaceous groundcover may be greater than in the tabonuco forest.

Tree Growth.—Compared to virgin tabonuco stands, growth in virgin colorado stands is slow. For example, the average annual volume increment in the colorado forest was 2 m³/ha and in the tabonuco forest 4.2 m³/ha (Tropical Forest Experiment Station 1953). Because growth rates in virgin colorado stands are slow, large trees have been estimated to be very old. Colorado trees of 10 cm dbh were estimated to

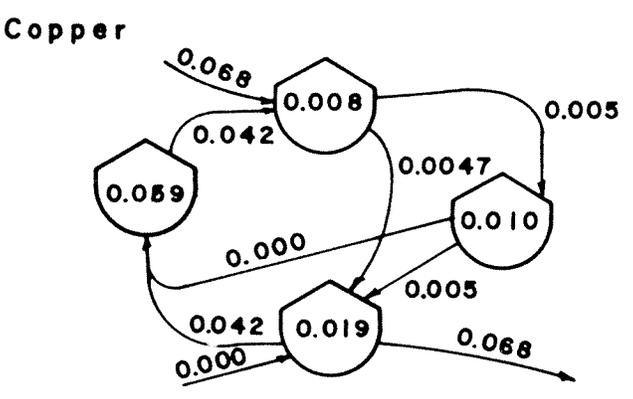
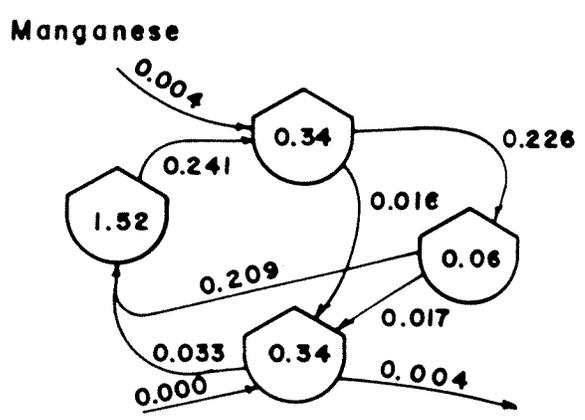
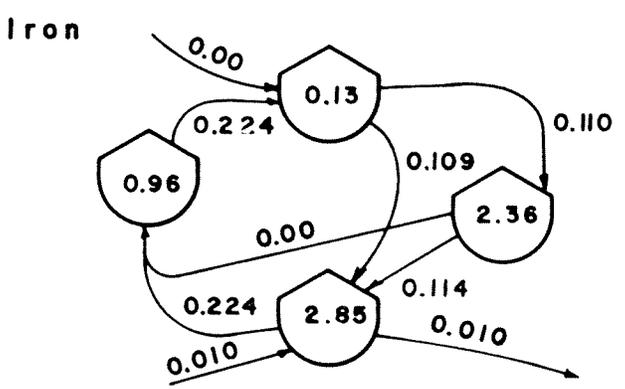
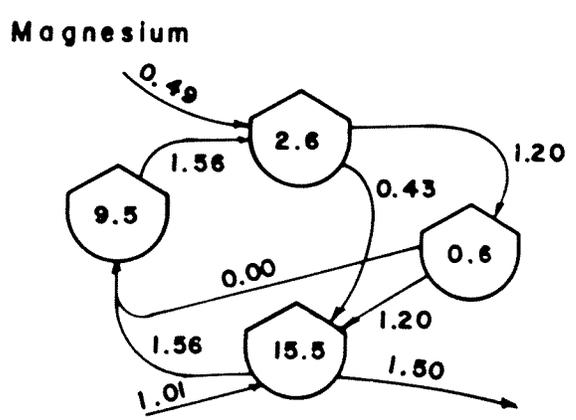
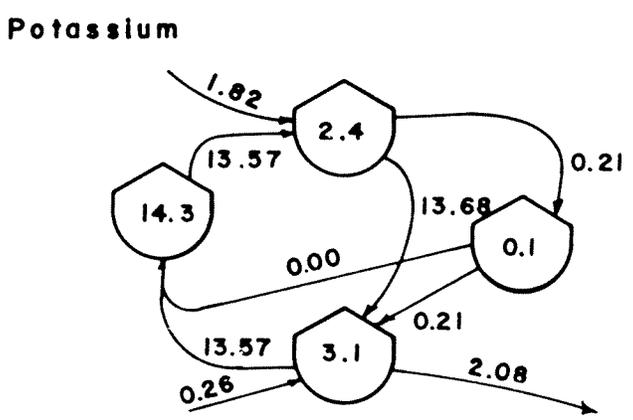
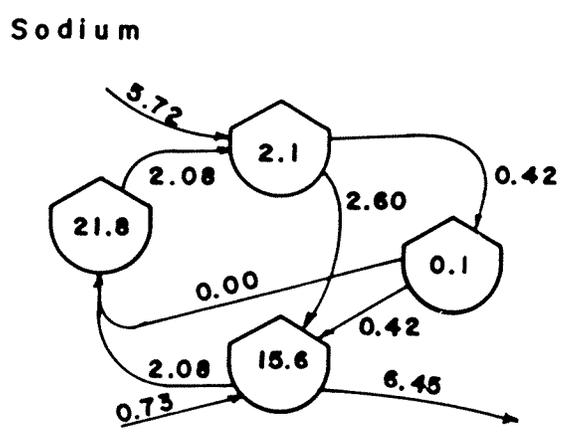
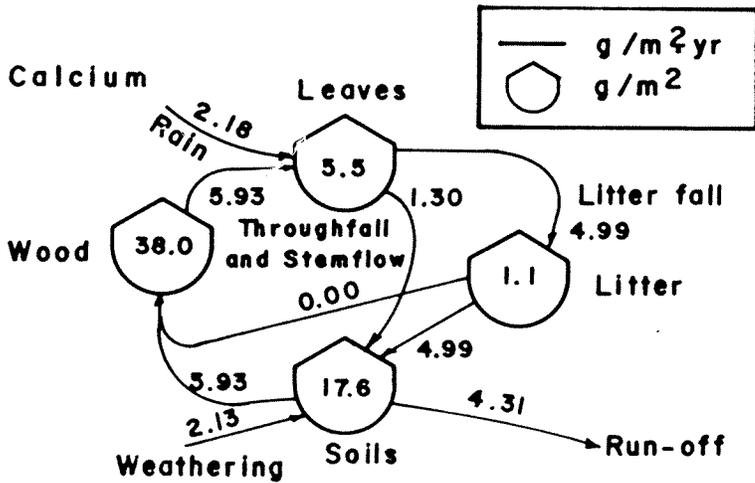


Figure 50.—Estimates of mineral cycles in the tabonuco forest at El Verde (Jordan et al. 1972).

in the compartments, standard error of the mean, and total stable strontium and manganese in each compartment (Jordan et al. 1973)

Compartment	Mass (kg/ha)	Concentration			Total element (kg/ha)	
		n	(ppm)		Sr	Mn
			Sr	Mn		
Stem	153,310	288	14.9 ± 0.62	53 ± 3.40	2.28	8.12
Branch	36,770	—	—	—	0.54	1.95
Root	72,300	72	18.7 ± 0.85†	71 ± 6.60†	1.35	5.13
Total woody parts	262,380				4.17	15.20
Leaves	9390	288	36.0 ± 1.91	360 ± 17.26	0.39	3.38
Litter	3800	24	30.3 ± 2.42	167 ± 21.00	0.12	0.63
Soil	124 (10 ⁴)	48	7.15 ± 0.98*	2.79 ± 0.47*	8.86	3.45

*Extract.

†Concentrations in branches assumed to be equal to concentrations in stems.

Table 50b.—Flux of water, and leaves and litter through the ecosystem, average concentration of elements in these fluxes, plus or minus the standard error of the mean,* and total element fluxes through the ecosystem (Jordan et al. 1973)

Flow	Carrier flux [(kg/ha-week) (10 ³)]	Average yearly concentration†		Element flux [(kg/ha-week) (10 ⁻³)]	
		[ppm (10 ⁻³)]		Sr	Mn
		Sr	Mn		
Rain	611	4.52 ± 0.10	1.24 ± 0.03	2.76	0.76
Evaporation from leaves	98				
Throughfall	404	8.72 ± 0.03	5.58 ± 0.02	3.52	2.25
Stemflow	109	6.8 ± 0.02	13.46 ± 0.04	0.70	1.47
Leaf and litter fall	0.105	60500.00 ± 1241	414000.00 ± 8083	6.35	43.47
Into soil	513	20.60 ± 0.05	13.61 ± 0.03	10.57	6.98
Transpiration	255				
Runoff	258	12.27 ± 0.07	2.96 ± 0.02	3.16	0.76

*Number of pooled samples = 12.

†The error terms may appear small to experienced workers. The terms are small because a lot of the variation in concentrations which occurred during a single storm or series of storms was eliminated by the pooling procedure.

be 80 yr old and those of 91 cm dbh to be 1,200 yr old (Tropical Forest Experiment Station 1953). In contrast, tabonuco trees of 91 cm dbh were estimated to be only 420 yr old.

Palm Forest

The sierra palm (*Prestoea montana*) dominated forests found at elevations similar to the colorado but in areas where slopes are steeper and soils wetter, was first designated as 'palm-brake' by Beard (1949). The sierra palm is also an abundant component of the understory and canopy of both the colorado and tabonuco type forests and is considered an indicator species of both.

Physiognomy.—Species in the palm forest include those found in both the tabonuco and colorado forests with only seven species being more common in the palm forest than elsewhere. On Mt. Britton the sierra palm comprised 61% of the canopy species (table 57).

The palm, which may reach 15 m in height, comprises a large proportion of the single tree strata. Sierra palm trees have small diameters; 75% of the trees sampled were in the 10–25 cm diameter classes (table 58). Herbaceous vegetation, vines and epiphytes are relatively scarce.

Autecological Study of Sierra Palm.—Beard (1949) originally described these palm forests as successional vegetation. However, radial growth rates

Table 51.—Mean annual standing crop of leaf detritus, mean annual leaf fall, and mean annual rate of disappearance of leaf detritus in the tabonuco forest at El Verde (Wiegert 1970a)

	Radiation center	Control center	Mean
Standing crop (g/m ²)	685	511	
Disappearance rate (g/g-year)	0.850	0.519	
Annual disappearance (g/m ²)	705	265	485
Annual leaf fall (g/m ²)			
Year 1	501	472	
Year 2	480	483	
\bar{x}	491	478	485

were found to be one of the slowest in the forest (Tropical Forest Experiment Station 1951). For this reason and because of its structural importance in the tabonuco forest, Bannister (1970) investigated the ecological life history of the species. The low light requirement for germination and seedling growth, long seedling survival in the forest and slow growth rates were all characteristics attributed to climax, rather than successional species. Size class distribution in the tabonuco forest indicates that the greatest mortality occurs between the young tree and canopy stages (fig. 57). It may be that sufficient light given at this critical stage in the life cycle and its ability to anchor securely by numerous above ground roots account for the dominance of sierra palm in areas of steep slopes and saturated soils.

Bannister (1970) estimated that the sierra palm may produce as many as 150,000 seeds during its reproductive lifetime. Maximum flowering occurred between June and September and peak fruiting between October and February (fig. 58).

Tree Growth.—Annual height growth increased along a gradient from trees in the canopy position to trees in the understory position (considering trees in the less vigorous class (2) only; table 59). This reversal of the usual relationship found for tree growth may be explained by a variation in growth rate as a function of age (Tropical Forest Experiment Station 1952). The low-canopy position trees are very young and the canopy trees are older. Trees in the most vigorous class (1) grew about 40–80% faster than less vigorous trees at the same position in the forest.

Dwarf Forest

This forest type is also referred to as the cloud forest, elfin forest, and mossy forest. Found on the summits of mountains in the Luquillo Experimental Forest, it is composed of dense stands of short, small diameter, twisted trees and shrubs. The plants and

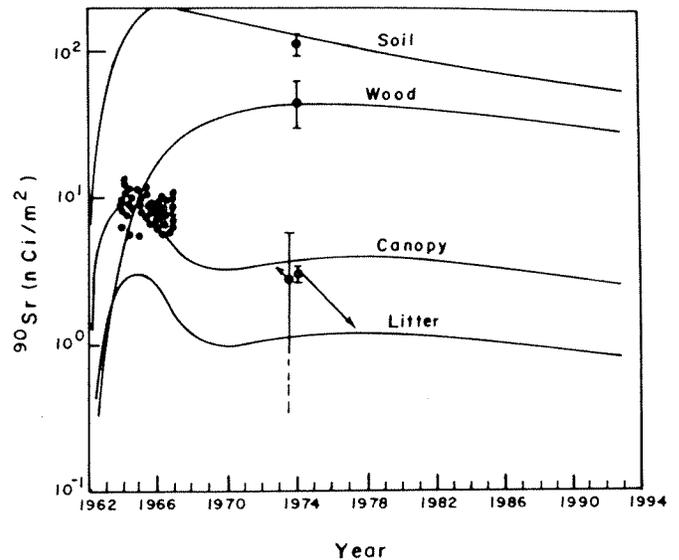


Figure 51.—Predictions of total amount of ⁹⁰Sr in various compartments of a tropical rain forest for 1962 through 1994, and validation points for 1964–1967, and 1974. Data points show 1 S.D. (Jordan and Kline 1976).

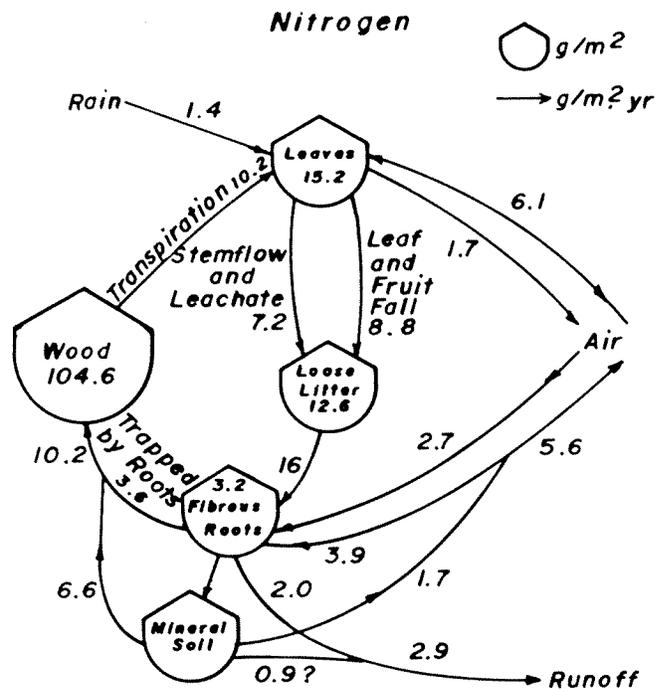


Figure 52.—The nitrogen budget in the tabonuco forest at El Verde (Edmisten 1970e).

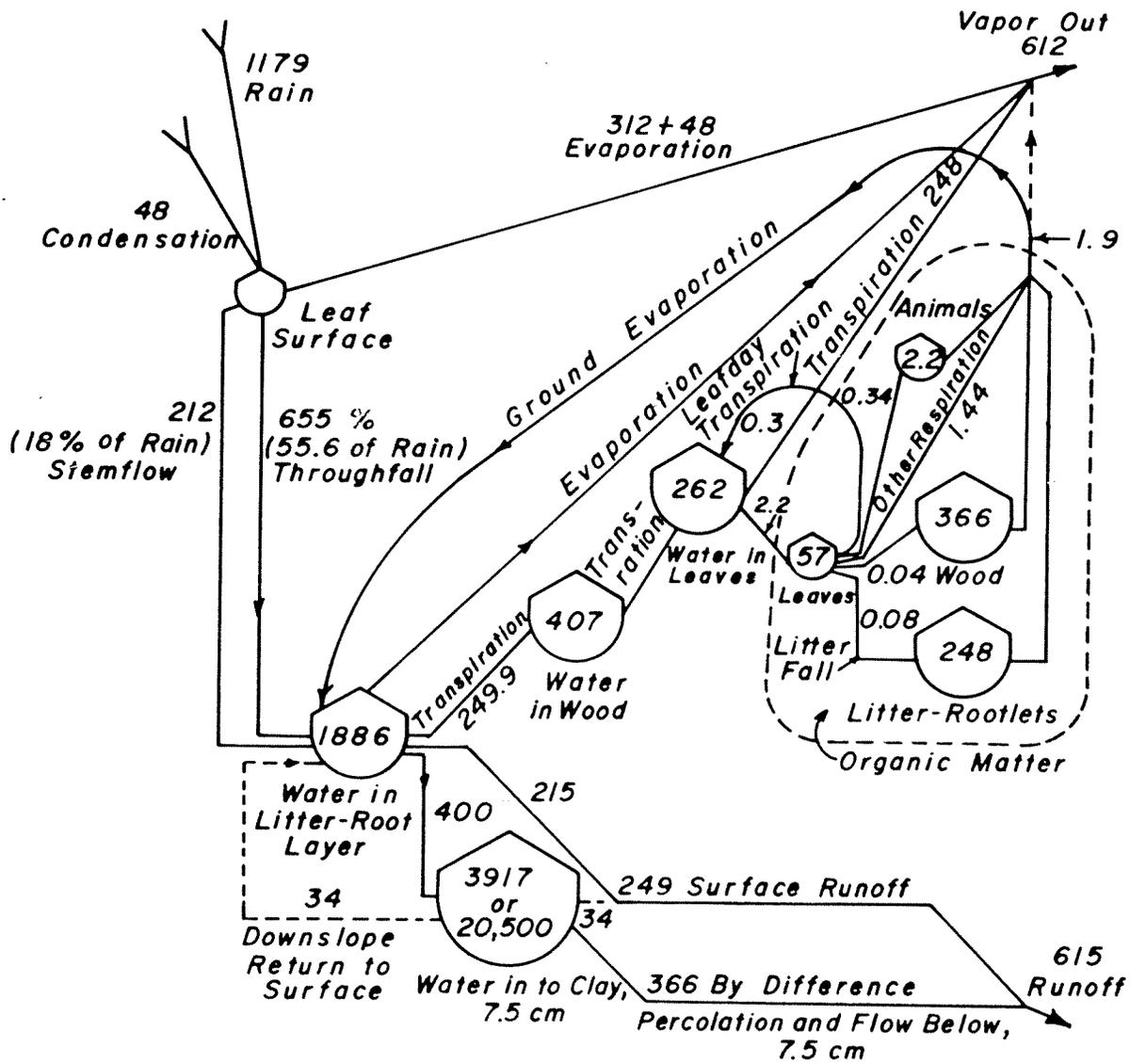


Figure 53.—Hydrogen budget in the tabonuco forest at El Verde. Storages are in $g\ H/m^2$ and flows in $g\ H/m^2\text{-day}$ (Odum et al. 1970e).

Table 52.—Nuclide retention by leaves with and without epiphylls in the tabonuco forest at El Verde (Witkamp 1970)

Species	Epiphylls†	$^{137}Cs^*$	^{32}P	^{54}Mn	^{89}Sr
<i>Ormosia krugii</i>	+	1054	336	878	6
	—	9	18	5	2
<i>Euterpe globosa</i>	—	116	18	186	3
	+	1061	253	956	7
<i>Dacryodes excelsa</i>	—	20	10	2	2
	—	53	24	416	3
<i>Manilkara bidentata</i>	+	1726	218	386	7
	—	12	17	2	2
Young leaf	—	148	13	155	4
	+	1193	408	632	10
Young leaf	—	7	5	2	3
	—	182	86	370	4
	—	39	70	496	4

*Numbers in left column under each nuclide are parts per million of nuclide in solution retained by each disk. Right column shows the ratio of radioactivity retained by disks with epiphylls to the amount of radioactivity retained by disks without epiphylls.

†+ indicates with epiphylls; — indicates without epiphylls.

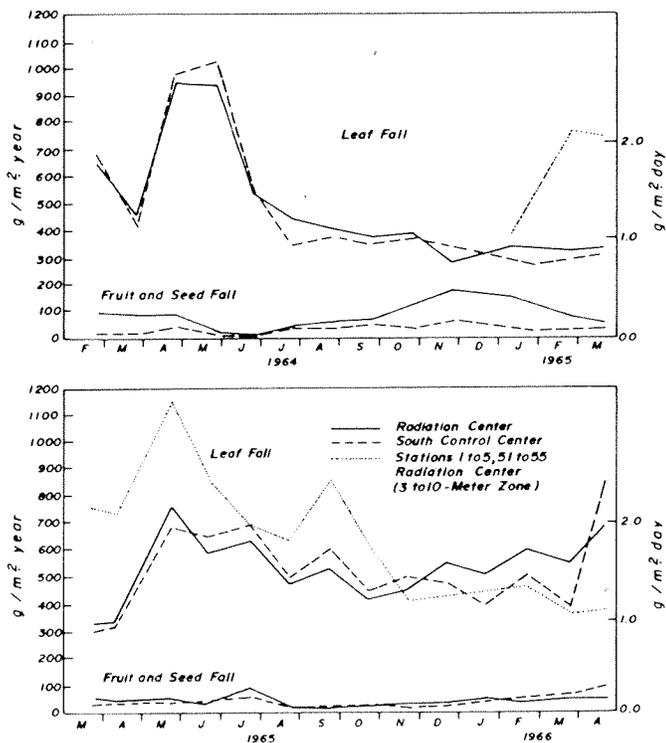


Figure 54.—Seasonal and annual variation in rate of leaf, fruit, and seed fall in the tabonuco forest at El Verde (Wiegert 1970a).

forest floor are covered with mosses and epiphytes. The vegetation is exposed to winds and usually shrouded with clouds. Research on the dwarf forest has been restricted to the areas on Pico del Este (Odum and Cintrón 1970; Weaver 1972 and 1975; Byer and Weaver 1977) and on Pico del Oeste by the Arnold Arboretum (1968–1977).

Climate of Pico del Oeste.—Monthly rainfall at Pico del Oeste ranged from a low in January of approximately 30 cm to an average high throughout the summer months of approximately 45 cm (fig. 59a). The highest rainfall of 60 cm/mo was recorded in December. Relative humidity varied little over the annual cycle ranging from 95–100% (fig. 59a). Mean monthly temperature varied from 16.5°C in January and February to a high of 20°C in October (fig. 59b). The difference between the mean minimum temperature and the mean maximum temperature of the air was approximately 3.5°C. However, the difference between the mean minimum and mean maximum temperature of the soil was lower (2.5°C). Soil temperature was approximately 0.5°C cooler than air temperature in the summer months, but in the winter months, soil temperature was approximately 0.5°C warmer than air temperature. Maximum solar radiation occurred in April (approximately 320 langleys/day) and minimum solar radiation occurred in May (approximately 200 langleys/day; fig. 59c). Solar ra-

diation from June through October varied little ranging from 250–290 langleys/day.

Physiognomy.—The three most common species of plants at Pico del Oeste were an herb (*Pilea krugii*), followed by a semi-woody plant (*Wallenia yunquensis*), and a woody canopy plant (*Calycogonium squamulosum*); woody canopy plants dominated the remaining seven of the ten most common plants (table 60). A list of all plants found at Pico del Oeste by Howard (1968) is given in table 61. Woody emergents are by far the most abundant life form. Two species dominated the canopy, accounting for 71% of the canopy cover (table 62). A profile of the dwarf forest, along an approximate 9 m transect is shown in figure 60.

The dwarf forest is located on windward, ridge, and leeward areas of the mountain tops (table 63). On the ridges trees were shorter and with smaller diameters whereas in the leeward zone, trees were taller and had larger diameters (table 63). The number of tree species and stem density decreased along the gradient of windward to leeward locations. Basal area, however, was highest in the leeward zone and lowest on the ridge. A significant quantity of trees in all three sites was dead (8–15%), with most of the dead trees occurring on the ridge. The largest proportion of trees at all three areas are in the 2.5–4.8 cm diameter class (fig. 61). Less than 10% of the trees on the windward and ridge sites are in the 7.6–22.6 cm diameter classes. The leeward site has proportionally more larger trees than the other two sites.

Biomass.—Total leaf biomass for a site at Pico del Oeste, was estimated at 288 g/m², with a Leaf Area

Table 53.—Mean populations of microfungal propagules (per g leaf sample) on leaves taken from three heights of two tree species in the tabonuco forest at El Verde (Cowley 1970c)

	<i>Dacryodes</i>	<i>Manilkara</i>
Top	93,800 ± 12,194	29,300 ± 14,168
Midpoint	71,600 ± 23,048	163,800 ± 32,636
Bottom	106,500 ± 28,714	283,300 ± 72,201

Table 54.—Number of species of microfungi on leaves taken from three heights of two tree species in the tabonuco forest at El Verde (Cowley 1970c)

	<i>Dacryodes</i>	<i>Manilkara</i>
Top	19	28
Midpoint	29	40
Bottom	33	36

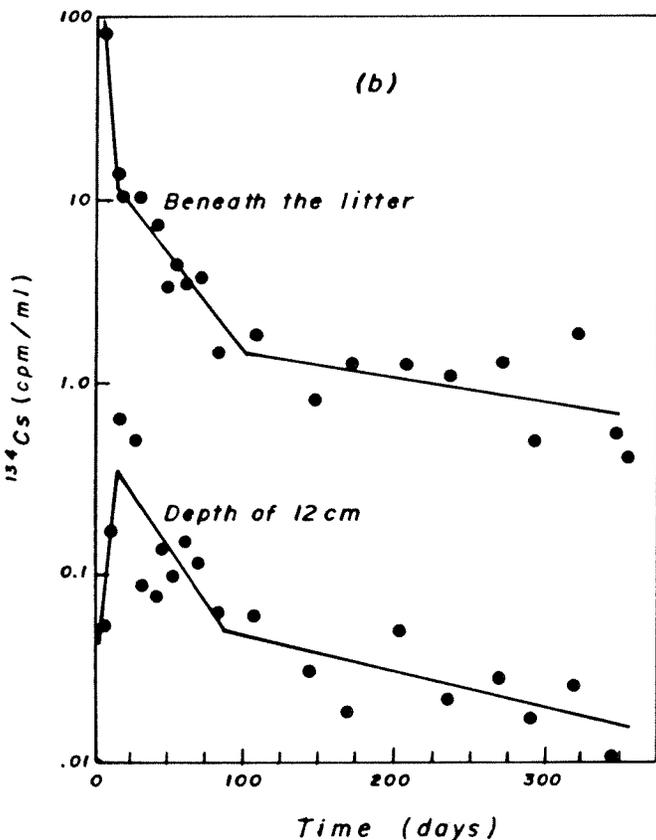
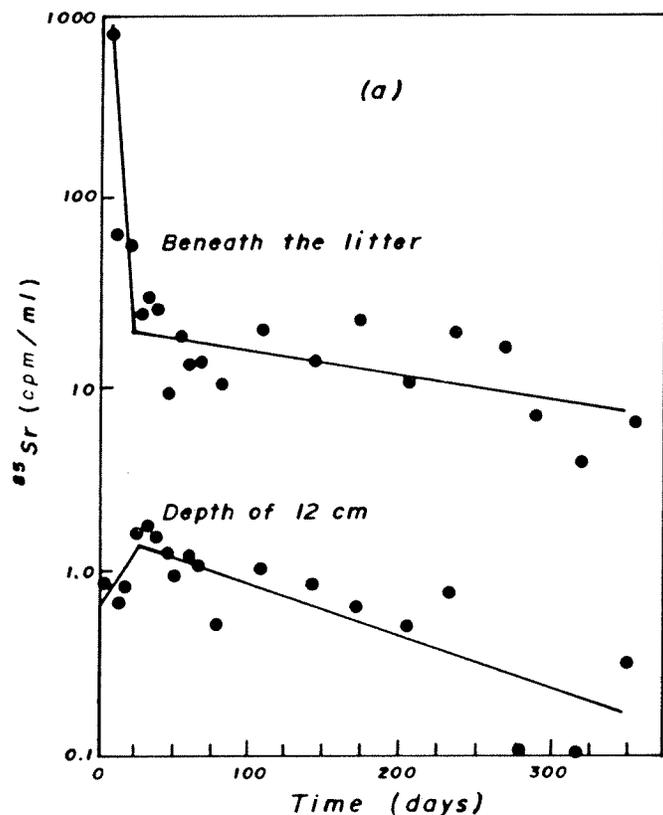


Figure 55.—Activity of (a) ^{134}Cs and (b) ^{85}Sr in the soil water collected beneath the litter and at a depth of 12 cm (Jordan 1970b).

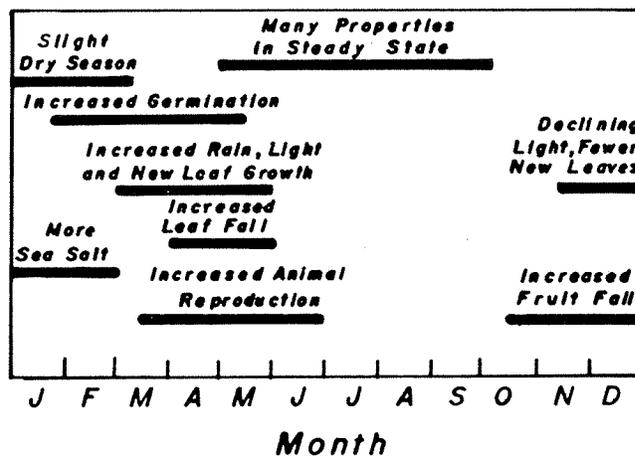


Figure 56.—Calendar of seasonal events in the tabonuco forest (Odum 1970b).

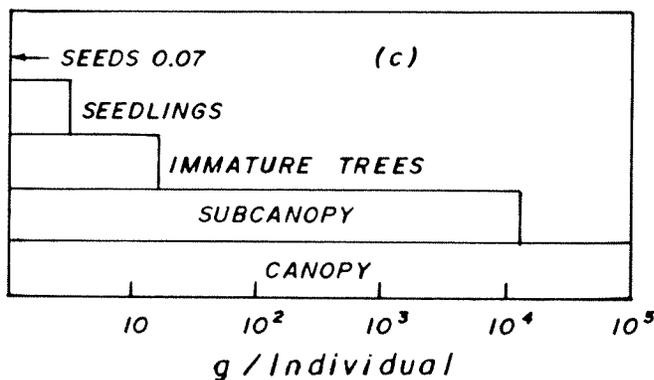
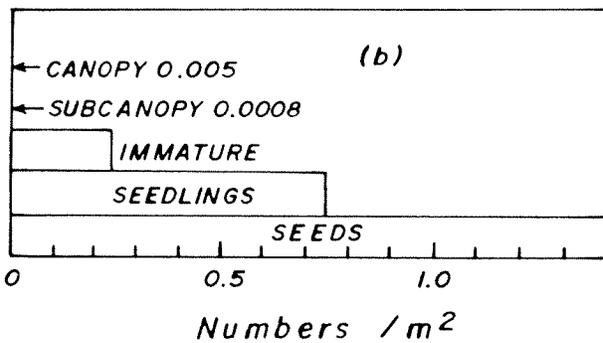
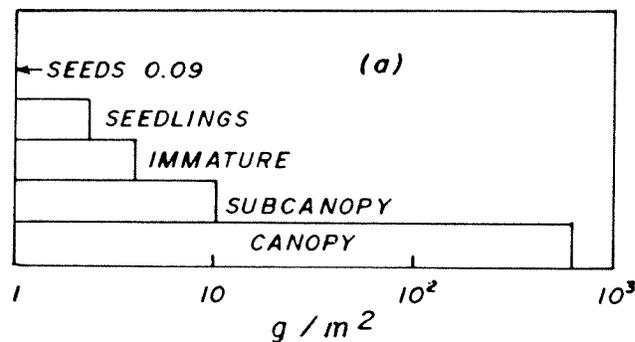


Figure 57.—(a) Sierra palm biomass (g/m^2) by size class, (b) sierra palm density by size class, and (c) sierra palm biomass per individual of each size class (Bannister 1970).

Table 55.—Number of species by size class in 4 ha of virgin colorado forest (Wadsworth 1951)

Species	Number of trees by dbh(cm)				Total
	10-15	20-25	30-35	40+	
<i>Cyrilla racemiflora</i> L.	29	22	43	82	176
<i>Micropholis garciniaefolia</i> Pierre	228	120	111	15	474
<i>Calycogonium squamulosum</i> Cogn.	239	122	81	3	445
<i>Euterpe globosa</i> Gaertn.*	873	12	885
<i>Micropholis chrysophylloides</i> Pierre	165	79	51	4	299
<i>Cecropia peltata</i> L.	47	12	9	68
<i>Magnolia splendens</i> Urban	22	7	6	11	46
<i>Croton poecilanthus</i> Urban	210	36	3	249
<i>Ocotea spathulata</i> Mez	62	33	17	1	113
<i>Tabebuia rigida</i> Urban	27	10	13	50
<i>Dacryodes excelsa</i> Vahl.	7	7	10	2	26
<i>Ilex nitida</i> (Vahl) Maxim.	29	6	10	1	46
<i>Inga laurina</i> (Sw.) Willd	18	2	8	28
<i>Sapium laurocerasus</i> Desf.	13	7	4	1	25
<i>Sloanea berteriana</i> Choisy	14	5	3	22
<i>Matayba domingensis</i> (DC.) Radlk.	22	5	2	29
<i>Eugenia stahlii</i> (Liaersk) Krug & Urban	7	10	2	19
<i>Homalium racemosum</i> * Jacq.	4	5	9
<i>Linociera domingensis</i> (Lam.) Knobl.	11	4	3	18
<i>Didymopanax morototoni</i> (Aubl.) Dcne.	9	7	2	18
<i>Cordia borinquensis</i> Urban	39	1	40
<i>Ocotea moschata</i> (Pavon.) Mez.	2	1	1	1	5
<i>Alchornea latifolia</i> Sw.	19	4	23
<i>Hirtella rugosa</i> Pers.	14	1	15
<i>Ditita myricoides</i> Griseb.	17	2	19
<i>Ficus laevigata</i> Vahl	5	3	1	9
<i>Ficus sintenisii</i> Warb	7	1	8
30 other species	159	30	22	1	212
Totals	2,298	548	408	122	3,376

**Prestoea montana*

Table 56.—Characteristics of tabonuco and colorado forests in the Luquillo Experimental Forest (Smith 1970b)

Features	Colorado	Tabonuco
Tree species for an average 4 ha	51	73
Dominant indicators	<i>Micropholis garciniaefolia</i> , <i>Cyrilla racemiflora</i>	<i>Dacryodes excelsa</i> , <i>Sloanea berteriana</i>
Maximum height	20 m	30 m
Deciduousness	No species	Several species
Compound-leaved species	None	24%
Flowering and fruiting	Never heavy	Most species with a large production
Mean leaf width of the species in the shade corrected for species relative densities	4.5 cm	10.0 cm
Mean leaf thickness of the species in the shade	0.45 mm	0.28 mm
Lianas	More common	Less common
Bromeliads in the canopy	Common	Less common
Herbaceous ground growth	Often a complete cover	Little cover, mainly tree seedlings

Index of two (Dugger 1977). No data are available for the woody biomass. However, biomass of understory plants at a site at Pico del Oeste was higher than the estimated leaf biomass measured by Dugger (1977) (table 64). Plants on the forest floor were primarily algae and liverworts. Biomass of leaf litter and twigs on the forest floor is low (table 64), but it completely covers the floor (Lyford 1969). Surface roots lie in a layer between the litter and the 02 horizon, forming a mat 2–2.5 cm thick (Lyford 1969). These surface roots comprise 60% of the total forest floor biomass. Lyford (1969) found that some tree roots extend 7–8 m laterally, a greater distance than the tree height. He also found 80–90% of the roots in the upper 10 cm of soil.

The amount of plant material on tree stems (390 g/m², excluding the soil-like material) is similar to

the amount of plant material on the forest floor (392 g/m², excluding the roots; table 65). Liverworts were the main constituent of the plant material on tree stems. The soil-like material on stems is probably the result of decay of plants; most of this material lost 90–95% of the weight upon ignition (Lyford, 1969).

Leaf Characteristics.—The majority of all the plants in the dwarf forest at Pico del Oeste had microphyllous leaves regardless of their habitat type (table 66 and 67). Ninety-four percent of all leaves were between 0.25 cm² and 182 cm².

Stomata of leaves from a variety of dwarf forest plants were larger than stomata of lowland leaves (fig. 62). The number of stomata per unit area of leaf was also greater in the dwarf forest; dwarf forest leaves had a mean number of stomata of $46 \times 10^3/\text{cm}^2$ based on 8 species while the lower montane forest had $28 \times 10^3/\text{cm}^2$ based on 14 species (Cintrón 1970). More numerous and large stomata are possibly adaptations to maximize transpirational rates in high humidity environment (Cintrón 1970).

Chlorophyll a.—Mean chlorophyll *a* concentration in leaves of plants from Pico del Oeste was 1.5–2 times higher than in leaves from climax and succes-

Table 57.—Species composition of palm forest at Mt. Britton (Recher 1970a)

Species	Composition (%)
Canopy species	
<i>Euterpe globosa</i> *	61.0
<i>Croton poecilanthus</i>	15.0
<i>Calycogonium squamulosum</i>	10.0
<i>Cordia borinquensis</i>	7.0
<i>Psychotria berteriana</i>	†
<i>Hillia parasitica</i>	†
<i>Cecropia peltata</i>	†
<i>Ocotea leucoxydon</i>	†
<i>Micropholis garciniaefolia</i>	†
<i>Miconia sintenisii</i>	†
Understory trees and shrubs	
<i>Daphnopsis philippiana</i>	†
<i>Comocladia glabra</i>	†
<i>Hedyosmum arborescens</i>	†
<i>Cyathea pubescens</i>	†
<i>Cesneria sintenisii</i>	†
Lianas and woody vines	
<i>Schlegelia brachyantha</i>	†
<i>Clusia gundlachii</i>	†
<i>Marcgravia sintenisii</i>	†
<i>Ipomoea repanda</i>	†
Terrestrial herbs	
<i>Dryopteris deltoidea</i>	†
<i>Alsophila borinquena</i>	†
<i>Pilea krugii</i>	†
<i>Pilea inaequalis</i>	†
<i>Begonia decandra</i>	†
<i>Ichnanthus pallens</i>	†
<i>Scleria</i> sp.	†
Epiphytes	
<i>Nephrolepis rivularis</i>	†
<i>Guzmania berteroniana</i>	†

**Prestoea montana*

†Present

Table 58.—Stand density in a virgin palm forest (Wadsworth 1951)

Diameter at breast height (cm)	Stem density (no./ha)
10–15	138.1
20–25	180.8
30–45	11.9
50 +	2.8
Total	333.6

Table 59.—Growth of sierra palm (*Tropical Forest Experiment Station* 1952)

Position in forest	Vigor class ^a	Number of trees	Annual height growth (cm)
Canopy	2	25	10.0
Canopy	2	34	13.7
Mid-canopy	1	10	26.5
	2	99	14.9
Low-canopy	1	21	22.3
	2	95	15.9

^a1 is most vigorous, based on crown size and leaf color.

Table 60.—The ten most common species represented in these transect studies were the following, in order of frequency. The second figure given represents the number of seedling plants. (Howard 1968)

1. <i>Pilea krugii</i>	1376	Terrestrial herb
2. <i>Wallenia yunquensis</i>	1120–40	Semi-woody, terrestrial
3. <i>Calycogonium squamulosum</i>	1063–224	Woody, canopy plant
4. <i>Vriesia sintenisii</i>	978	Epiphyte
5. <i>Ocotea spathulata</i>	904–297	Woody, canopy plant
6. <i>Calyptranthes krugii</i>	807–140	Woody, canopy plant
7. <i>Pilea obtusata</i>	731	Herb restricted to palm glades
8. <i>Dilomilis montana</i>	717	Epiphyte
9. <i>Miconia pachyphylla</i>	433–25	Woody, canopy plant
10. <i>Cyathea pubescens</i>	386	Woody, sub-canopy plant

sional species from the lower montane or tabonuco forest (fig. 63). The Leaf Area Index of this dwarf forest site was 2.7, resulting in a total chlorophyll content of the forest of 1.7 g/m² ground surface (Odum and Cintrón 1970). Although the dwarf forest appears greener than the lower tabonuco forest, there is less chlorophyll in the total vertical column of the dwarf forest. For example, total chlorophyll *a* in the vertical column of the tabonuco forest ranged from 2.1–2.7 g/m² ground surface (Odum and Cintrón 1970).

Aerial Roots.—Roots of plants in the dwarf forest are found in the soil profile, immediately above the soil surface in the litter layer, appressed to trunks and branches of trees, and hanging freely in the air (Gill 1969). Many of the trees, shrubs, vines, and herbs have freely hanging aerial roots. The aerial roots of trees and shrubs were generally flexible, 1–2 mm thick, growing from stems of approximately 5 mm diameter, and within 50 cm of the leaf zone (table 68). Very few of the aerial roots were without injury. Aerial roots of vines were in the leaf zone, and were generally very thin (maximum diameter of approximately 0.3 mm) and flexible; most were also damaged (table 69). Herbs had aerial roots of similar size, flexibility and degree of injury to the aerial roots of vines (table 70). Lateral root development of herbs and vines was rare (Gill 1969).

Epiphytes.—Many trees and shrubs in the dwarf forest are covered with epiphytes. Weaver (1972) found that the mean epiphyte load for trees located in windward, ridge, and leeward sites was 555 g/m² (table 71). Epiphyte load on the trees at the windward site was significantly higher (1.6 times) than for trees in either the ridge or leeward sites. The epiphyte load of the trees was found to be exponentially related to the dbh of the tree (fig. 64).

A survey of epiphytic algae at Pico del Oeste was made (Foerster 1971) and more than 126 species,

belonging to 19 families were identified. The distribution of algal epiphytes with height on the stems of the major vascular plants shows two opposing trends, depending upon the time of year (fig. 65). In February–March the number of species was inversely related to the height above ground (fig. 65a), whereas in August the number of species was directly related to the height above ground (fig. 65b). These are probably related to differences in climate during the two sampling periods. During February–March rainfall was lower, the air temperature was cooler, and solar radiation was lower than in August (c.f. fig. 59). If humidity of the air is the limiting factor for the development of epiphytic algae, as suggested by Foerster (1971), then the higher rainfall and higher absolute humidity, as implied by the higher temperatures in August would provide more favorable conditions for the algae than those conditions in February–March.

Epiphytic mosses were sampled from nine trees, representing five species, at Pico del Oeste during the summer of 1967 (Russell and Miller 1977). Samples were collected from trunks, branches and leaves. Mosses were found on 126 samples (table 72); the 56 moss free samples were mainly from small branches and leaves in upper portions of the trees. The degree of cover and number of species of mosses decreased with increasing height on the tree (table 73). Most moss species occurred in the lower 25% of the trees (table 73). Tree species did not appear to in-

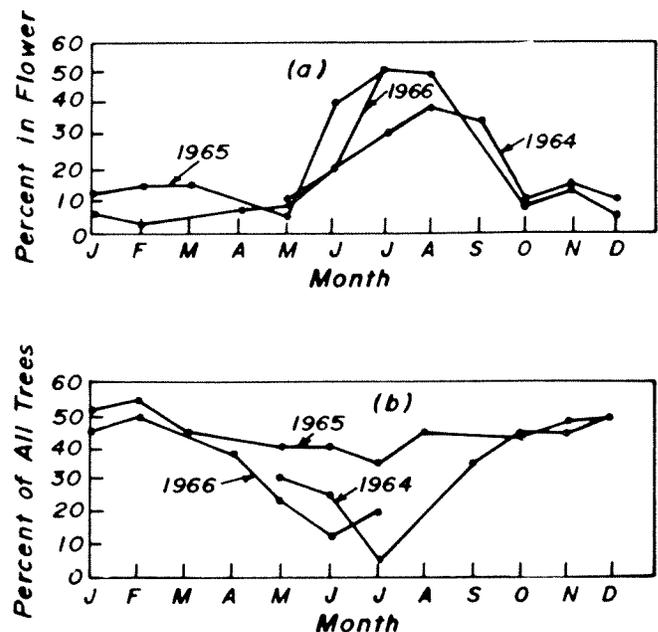


Figure 58.—Phenology of the sierra palm in the tabonuco forest. (a) Percent of trees in flower, and (b) percent of trees in fruit (Bannister 1970).

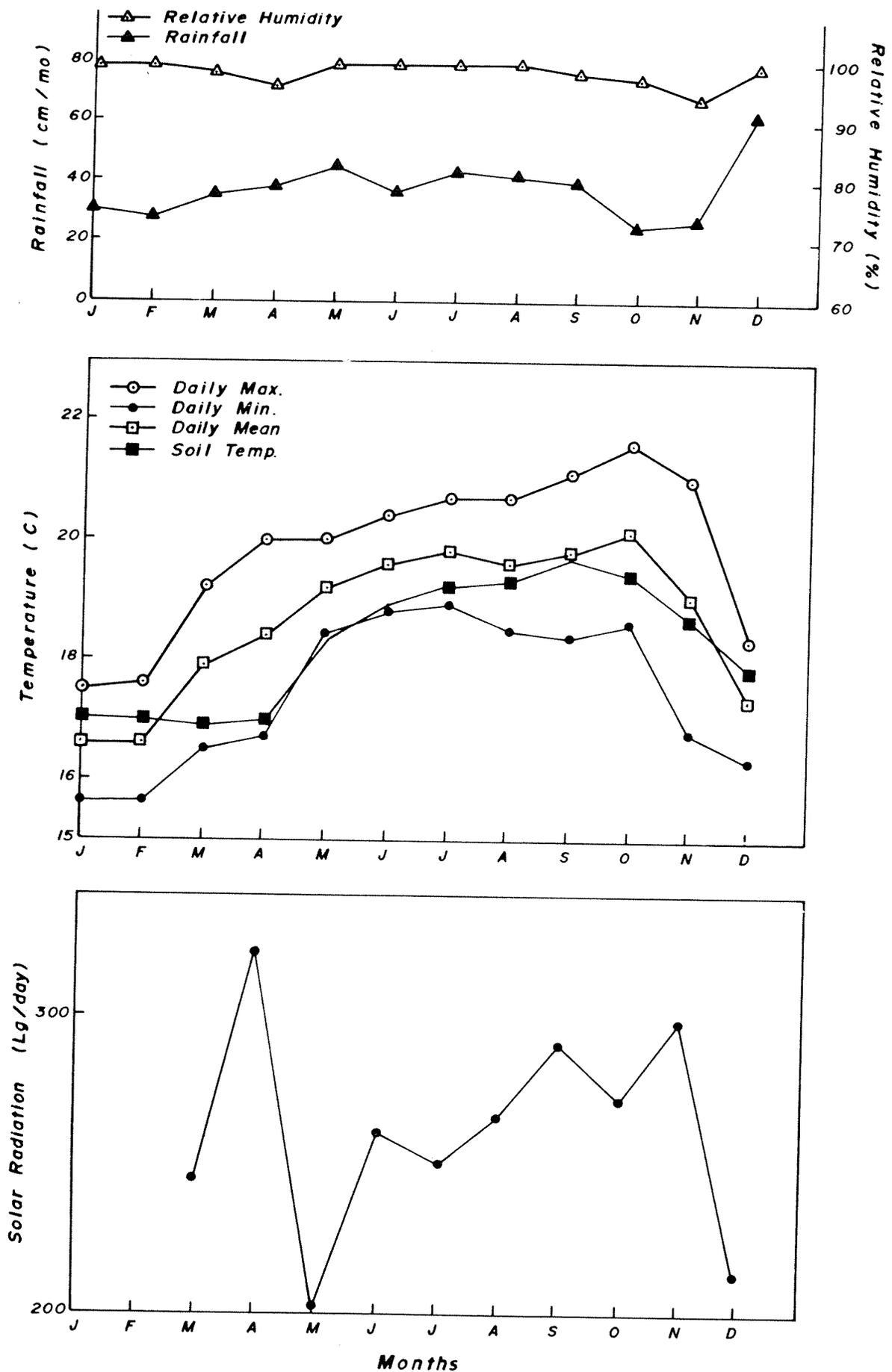


Figure 59.—Annual course of climatic variables at Pico del Oeste for the period March 1966 to February 1967 (Baynton 1968).

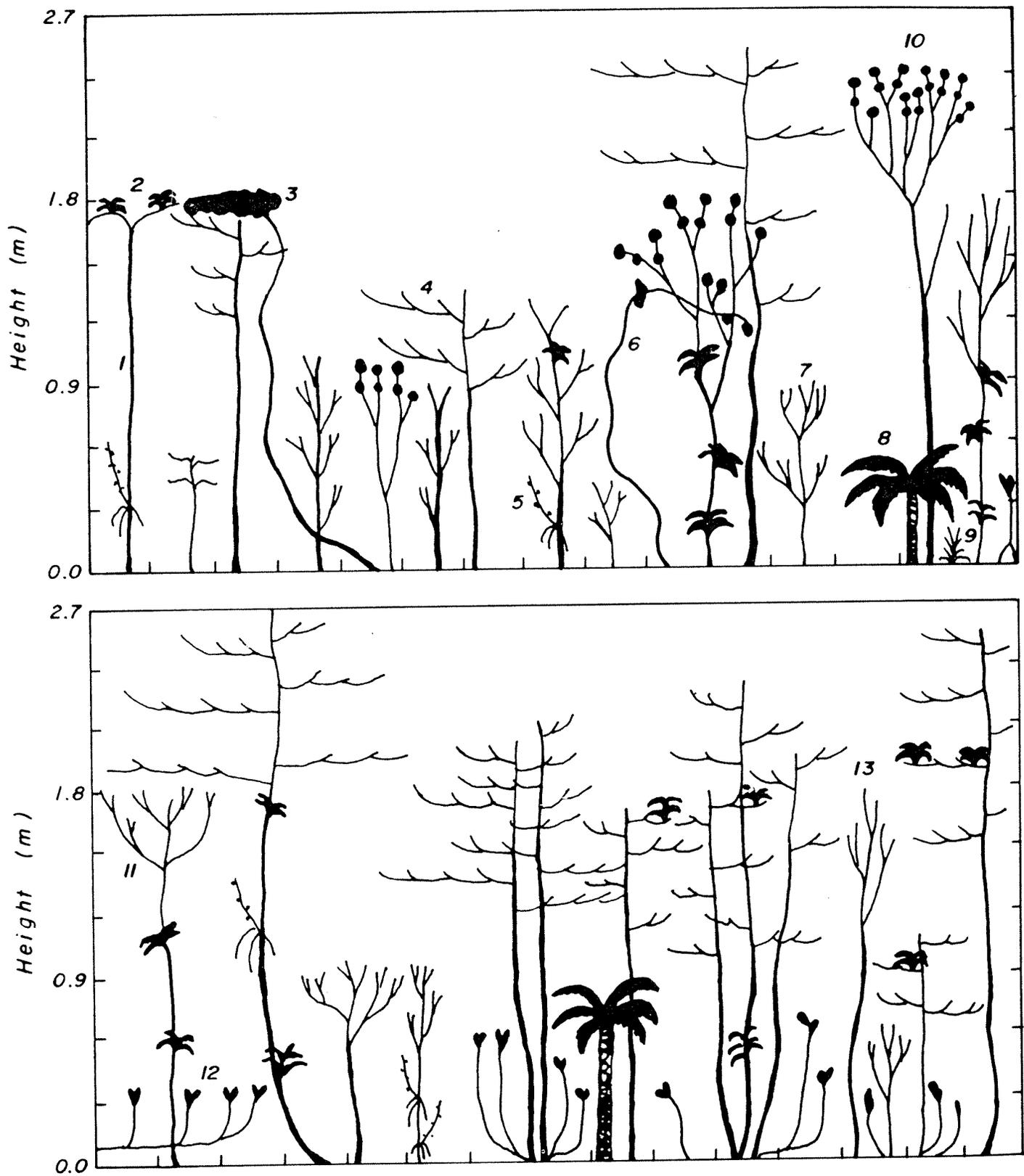


Figure 60.—Profile diagram of the dwarf forest at Pico del Oeste. Component species are: 1. *Miconia pachyphylla*; 2. *Vriesia sintenisii*; 3. *Marcgravia sintenisii*; 4. *Ocotea spathulata*; 5. *Dilomilis sintenisii*; 6. *Rajania cordata*; 7. *Calyptranthes krugii*; 8. *Cyathea pubescens*; 9. *Carex polystachya*; 10. *Eugenia borinquensis*; 11. *Tabebuia rigida*; 12. *Wallemia yunquensis*; 13. *Ilex sintenisii* (Howard 1968).

Table 61.—Species list for the dwarf forest at Pico del Oeste (Howard 1968)

Herbaceous			
<i>Pilea krugii</i>	1376	<i>Ichnanthus pallens</i>	110
<i>Pilea obtusata</i>	731	<i>Arthrostylidium sarmentosum</i>	32
<i>Pilea yunquensis</i>	297	<i>Scleria secans</i>	22
<i>Begonia decandra</i>	256	<i>Rencalmia antillarum</i>	5
<i>Carex polystachya</i>	168	<i>Justicia martinsoniana</i>	1
Epiphytes			
<i>Vriesia sintenisii</i>	978	<i>Alloplectus ambiguus</i>	11
<i>Dilomilis montana</i>	717	<i>Peperomia emarginella</i>	10
<i>Psychotria guadalupensis</i>	36-2	<i>Peperomia hernandiifolia</i>	10
<i>Anthurium dominicense</i>	13	<i>Hillia parasitica</i>	9-5
<i>Guzmania berteroniana</i>	11		
Woody emergents			
<i>Calycogonium squamulosum</i>	1063-224	<i>Ardisia luquillensis</i>	40
<i>Ocotea spathulata</i>	904-297	<i>Clusia grisebachiana</i>	38-5
<i>Calyptanthes krugii</i>	807-140	<i>Miconia pycnoneura</i>	33
<i>Miconia pachyphylla</i>	433-25	<i>Prestoea montana</i>	23-192
<i>Tabebuia rigida</i>	294-2	<i>Micropholis garciniaefolia</i>	24
<i>Eugenia borinquensis</i>	185-387	<i>Grammadenia sintenisii</i>	23
<i>Torrabasia cuneifolia</i>	104	<i>Symplocos micrantha</i>	19-3
<i>Ilex sintenisii</i>	98	<i>Cleyera albopunctata</i>	11
<i>Miconia foveolata</i>	91-47	<i>Haenianthus salicifolius</i>	4
<i>Trichilia pallida</i>	59	<i>Magnolia splendens</i>	1
<i>Hedyosmum arborescens</i>	58-1	<i>Rondeletia portoricensis</i>	1
<i>Mecranium amygdalinum</i>	46-34	<i>Miconia pycnoneura</i>	1
Undershrubs			
<i>Wallenia yunquensis</i>	1120-40	<i>Diplazium grandifolium</i>	48
<i>Cyathea pubescens</i>	386	<i>Psychotria berteriana</i>	35-2
<i>Gesneria sintenisii</i>	163-26	<i>Lobelia portoricensis</i>	12
Climbers			
<i>Marcgravia sintenisii</i>	154-117	<i>Mikania pachyphylla</i>	73
<i>Ipomoea repanda</i>	82	<i>Rajania cordata</i>	21
<i>Gonocalyx portoricensis</i>	82	<i>Hornemannia racemosa</i>	19

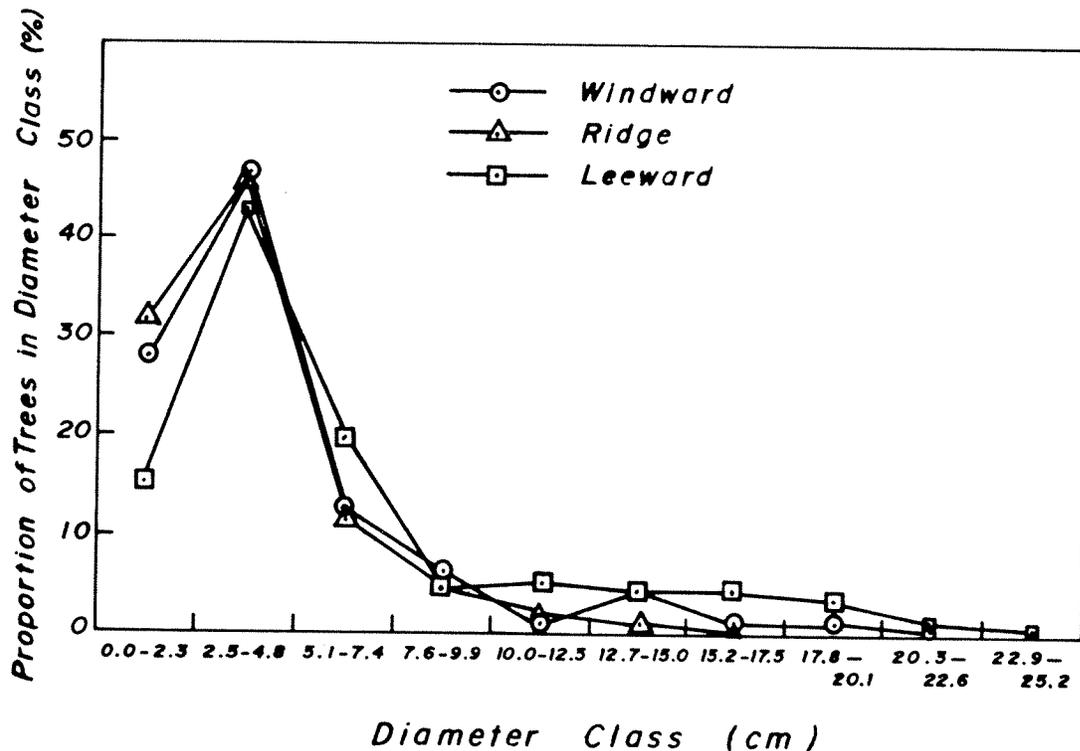


Figure 61.—Diameter class distribution of trees on the windward, ridge, and leeward areas of Pico del Oeste (adapted from Weaver 1972).

Table 62.—*Canopy species in the dwarf forest at Pico del Oeste (Howard 1968)*

Species	No. of plants in canopy	% of canopy
<i>Tabebuia rigida</i>	16	40.7%
<i>Ocotea spathulata</i>	46	30 %
<i>Calyptranthes krugii</i>	26	10.7%
<i>Calycogonium squamulosum</i>	13	4 %
<i>Marcgravia sintenisii</i>	7	4.2%
<i>Eugenia borinquensis</i>	7	4.2%
<i>Ilex sintenisii</i>	2	1 %
<i>Ardisia luquillensis</i>	2	3.9%
<i>Gonocalyx portoricensis</i>	4	
<i>Hedyosmum arborescens</i>	1	
<i>Mikania pachyphylla</i>	1	
<i>Psychotria guadalupensis</i>	1	

Table 63.—*Summary of forest parameters by working zone (adapted from Weaver 1972)*

Parameter	Average of three plots		
	Windward	Ridge	Leeward
Elevation (m)	1,000	1,015	930
Aspect	N 77 E	N 87 E	S 73 W
Slope (%)	53	37	26
Total no. tree species	13	12	8
Tree dbh (cm)	4.42	3.84	5.82
Basal area (m ² /ha)	42	32	54
Tree height (m)	3.3	2.8	4.0
Stem density (No./ha)	21,616	18,900	10,583
Dead stems (%)	8.3	15.2	11.0

Table 64.—*Biomass of components on the forest floor at Pico del Oeste (Lyford 1969)*

Component	Biomass (g/m ²)
Living plants	314
Leaf litter and twigs	78
Roots	577

Table 65.—*Amount of epiphytes and soil on tree stems at Pico del Oeste (Lyford 1969)*

Component	Biomass (g/m ²)
Living plants	265
Roots	125
Soil-like material	112

fluence the number and type of moss species (table 74). No particular moss species was dominant on any given tree as indicated by the low degree of cover (table 74). There appeared to be no definite trend in moss coverage or total number of species on windward and leeward surfaces of frees (table 75). However, constancy of species generally declined from leeward to windward surfaces.

Primary Productivity.—Some productivity data has been collected for the dwarf forest at Pico del Oeste, using CO₂ infrared analysis techniques in the field (Dugger 1977). Only estimates of gross primary productivity have been reported. The mean temperature during the period of Dugger's measurements was 18.6°C, which corresponds with the period of March-April or November-December (c.f. fig. 59). Dugger did not give the time of year that the measurements were made. Relative humidity is generally the lowest at these times of the year (c.f. fig. 59). Mean gross primary productivity for leaves in the dwarf forest was 3.4 g organic matter/m² leaf surface·day (Dugger's data was converted to g organic matter using the conversion factor of 4.5 kcal/g organic matter). Adjusting for the Leaf Area Index of two, total gross primary productivity for the dwarf forest was estimated to be 6.8 organic matter /m²·day. In comparison, gross primary productivity of the tabonuco forest at El Verde was 32.8 g organic matter/m²·day (Odum 1970b), and gross primary productivity of a subtropical dry forest in Puerto Rico was 3.2–10.4 g organic matter/m²·day (Lugo et al. 1978).

Herbivory.—In addition to predation of fruits by insects, leaves in the dwarf forest are also damaged to a considerable extent (table 76). Howard (1969) found that only young, succulent leaves were severely damaged. Insect damage reduced the leaf surface area by 16–35%. Mature leaves were often damaged by winds (Howard 1969).

Transpiration.—Transpiration rates for a variety of plants in the dwarf forest have been measured by Gates (1969), Weaver (1975), Weaver et al. (1973), and Dugger (1977). Gates (1969) determined transpiration rates by measuring leaf temperatures of several plants growing on the summit of Pico del Oeste. Transpiration was then estimated by means of an energy budget equation. For a relative humidity of 80% and a wind speed of 0.5 m/sec, transpiration rates varied linearly with temperature, ranging from 0.2 g/m² leaf surface·min at 14°C to 0.7 g/m² leaf surface·min at 19°C (the area of only one side of leaf was considered).

Weaver (1975) and Weaver et al. (1973) used freshly cut branches of a variety of species placed in potometers in both sun and shade in the forest to determine transpiration rates. All their results are ex-

pressed on a unit area of leaf surface based on the area of both sides of the leaf. Sun leaves transpired more than shade leaves, and successional species transpired more than climax species (table 77). However, the climax species were originally sampled from shaded portions of the forest which may have affected these results. The range of transpiration rates in sun was wider than in shade (table 78), possibly a result of more uniform climatic conditions within the forest due to attenuation of light and wind speed by the overhead canopy. Climatic conditions significantly affected transpiration rates (fig. 66). Transpiration rates increased linearly with increasing number of hours without cloud cover. Lack of cloud cover implies less humidity and thus greater saturation deficits. Using Weaver's (1975) mean transpiration rates for the sun and shade leaves (table 77 adjusted to the area of one side of the leaf) and the Leaf Area Index of two obtained by Dugger (1977), divided equally between sun and shade leaves, we calculated a mean daily transpiration rate of 440 g/m² ground surface (or 0.44 mm/day). Dugger (1977) enclosed portions of plants *in situ* in transparent chambers and, by measuring the difference in humidity of the air entering and leaving the chamber and correcting for air flow, he obtained transpiration rates of 560–870 g/m²

ground surface·day. In comparison, Odum and Jordan (1970) measured mean transpiration rates of 2136 g/m² ground surface·day for plants in the tabonuco forest. The values obtained by Dugger are higher than those measured by Weaver, but lacking information on the environmental conditions from Dugger, it is difficult to determine whether climate was the major cause for the difference.

The potometer, used in Weaver's (1975) study, measures water loss only by plant uptake. However, the method used by Dugger (1977) detects changes in moisture of the air as it flows over the plant, so his method measures water loss by plant uptake and evaporation of water of condensation. This difference in methodology possibly explains some of the differences in the two sets of results. The amount of water added to the dwarf forest by interception and condensation of cloud moisture by plants is significant and is equivalent to approximately 10% of rainfall (Baynton 1969; Weaver 1972). Therefore, the measurement of water losses from plants to the atmosphere by Dugger's method may be closer to the actual amount of water lost in terms of the balance of inflows and outflows. The low evapotranspiration rates from the forest explain why surface runoff from higher elevation streams is similar in quantity to the amount of rainfall falling on the peaks.

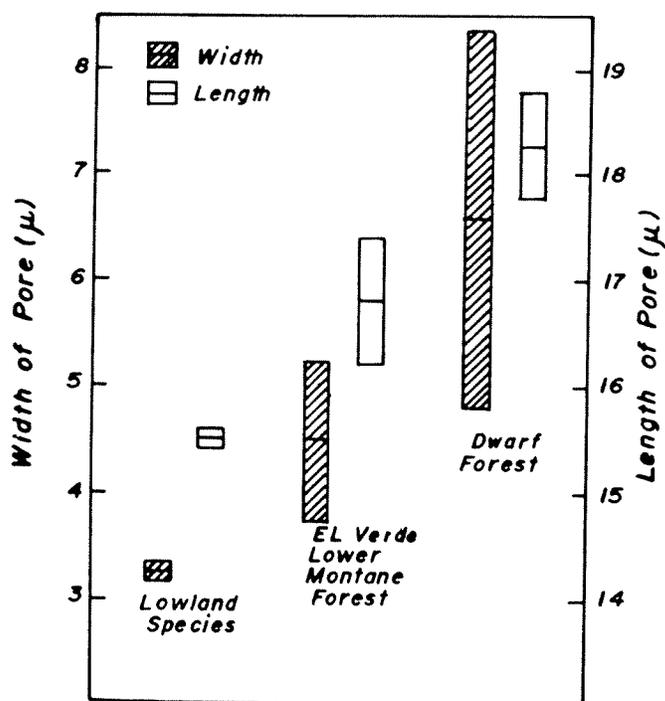


Figure 62.—Means of the length and breadth of stomata pores of the dwarf forest and other forest types. The horizontal line indicates the mean and the vertical bar represents one standard error (Cintrón 1970).

Table 66.—Size and distribution of leaves of plants at Pico del Oeste (Howard 1969)

Raunkiaer's leaf-size class	No. taxa	% of total
leptophylls ^a	1	1.9%
nanophylls ^b	6	11.5%
microphylls ^c	30	57.6%
mesophylls ^d	13	25.0%
macrophylls ^e	2	3.8%

^a<0.25 cm² ^b0.25 – 2.25 cm² ^c2.25 – 20 cm²
^d20 – 182 cm² ^e182 – 1,640 cm²

Table 67.—Classification of leaf-size by habitat (Howard 1969)

Leaf size	Vines-scramblers	Herbs	Epiphytes	Trees and shrubs
leptophylls	0	1	0	0
nanophylls	1	2	2	1
microphylls	3	10	2	15
mesophylls	1	2	2	8
macrophylls	0	0	1	1

Table 68.—*Properties of aerial roots of trees and shrubs (Gill 1969)*

Species	Tip properties				At root origin				
	Maximum diam. (mm.)	Maximum increment before laterals (cm.)	Maximum replacement tips	Color	Rigidity and alignment	Lateral roots without injury*	Minimum stem diam. (mm.)	Minimum distance to leaves (cm.)	Second. thick. before ground*
<i>Prestoea montana</i>	17	19	4	pale orange to pale pink	stiff & brittle, simple curves	+	58	45	—
<i>Hedyosmum arborescens</i>	3.5	80	3	white apex, then lemon, then green behind	unbent, flexible	—	4	5	+
<i>Ocotea spathulata</i>	6	36	4	pink to brown	unbent, flexible	—	12	30	+
<i>Trichilia pallida</i>	(1.2)	9	1	creamy brown to pink	unbent, flexible	—	7.5	15	?
<i>Ilex sintenisii</i>	0.7	5	3	white to brown	unbent, flexible	—	13.5	110	?
<i>Torrabasia cuneifolia</i>	0.6	12	5	orange	unbent, flexible	—	3	30	+
<i>Clusia grisebachiana</i>	6	89	2	white apex, yellow and brown behind	unbent, flexible	—	13.5	50	+
<i>Calyptranthes krugii</i>	1.2	14	1	white to red-brown	unbent, flexible	—	2.5	8	+
<i>Eugenia borinquensis</i>	1.8	24	1	white to red-brown	unbent, flexible	—	110	250	+
<i>Calycogonium squamulosum</i>	1.5	14	3	bright pink	unbent, flexible	—	4	2	+
<i>Mecranium amygdalinum</i>	1.2	9	2	white to pink	unbent, flexible	—	2	2	+
<i>Miconia foveolata</i>				pink		—	2	3	?
<i>Miconia pachyphylla</i>	0.9	10	2	white to pink	unbent, flexible	—	3.5	0	+
<i>Grammadenia sintenisii</i>	2.0	9	2	white to light brown	unbent, flexible	—	5	16	+
<i>Wallenia yunquensis</i>	1.0	10	4	white to pink	unbent, flexible	+	5	1	+
<i>Micropholis garciniaefolia</i>	2.7	17	?	white	unbent, flexible	—	47	150	?
<i>Symplocos micrantha</i>	0.8	4	6	white	unbent, flex, to hanging	—	5.5	6	+
<i>Haenianthus solicifolius</i>	1.5	23	6	cream ochre to brown	unbent to hang in cluster	—	8	15	+
<i>Tabebuia rigida</i>	2	10	5	creamy lime to weak yellow	unbent, flexible	—	11.5	6	+
<i>Gesneria sintenisii</i>	0.5	4	7	white to tan	unbent, flexible	—	3	3	?
<i>Psychotria berteriana</i>	0.7	7	2	beetroot to pale white	unbent, flexible	—	4	11	?
<i>Lobelia portoricensis</i>	1.5			white to pale green	unbent, flexible	—	7	0	?

* + represents presence, — represents absence.

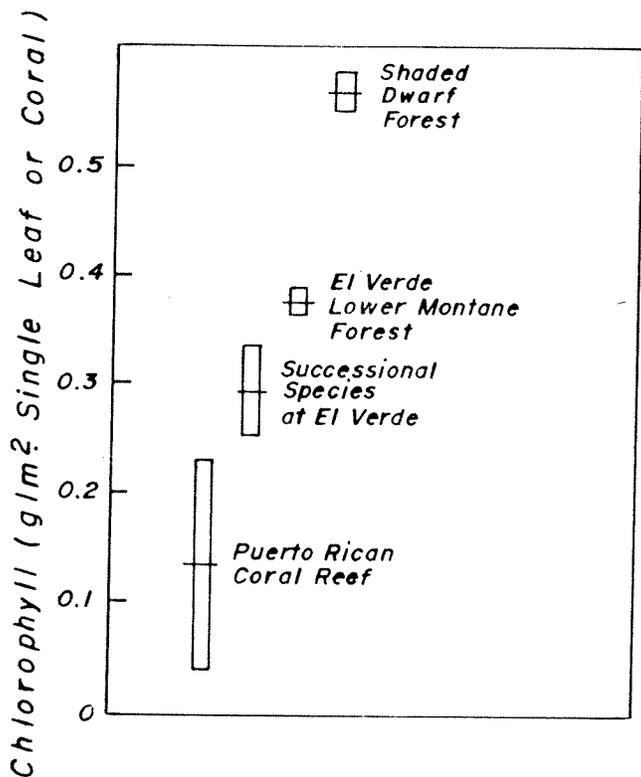


Figure 63.—Chlorophyll a of the dwarf forest and other ecosystems (Odum and Cintrón 1970).

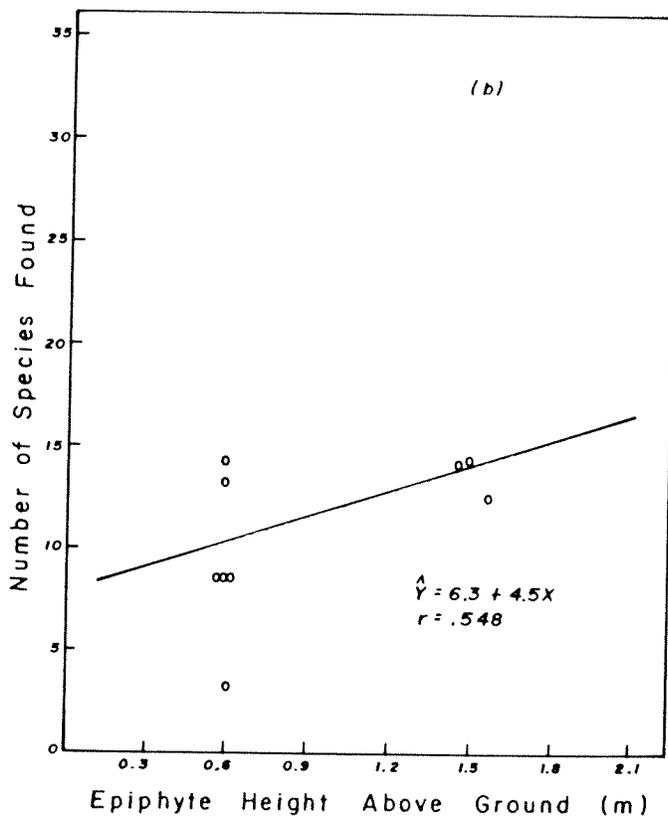
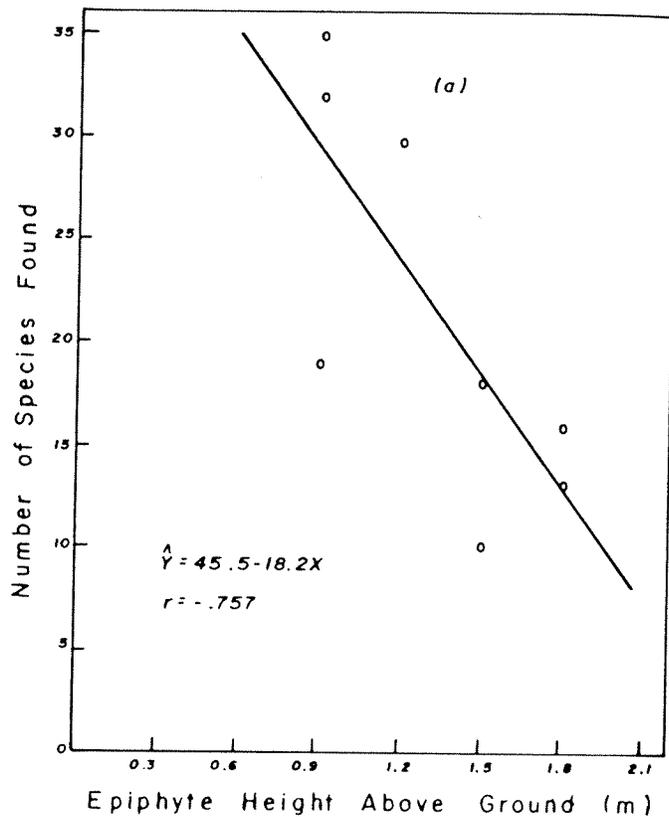


Figure 65.—Relationship between the height of collection on the vascular host to the number of epiphytic species found for the periods: (a) February-March 1966 and (b) August 1966. Samples were collected at Pico del Oeste (Foerster 1971).

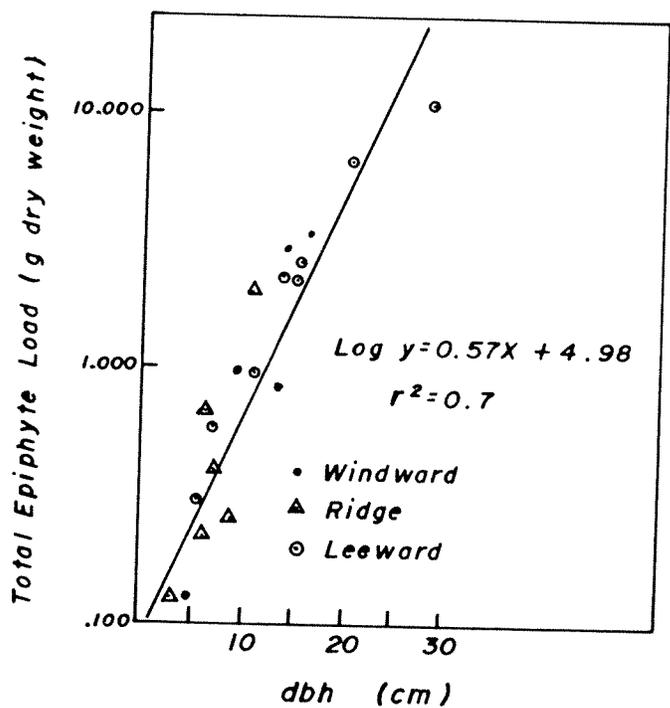


Figure 64.—Epiphyte load as a function of tree dbh for all trees regardless of location (Weaver 1972).

Table 69.—*Properties of aerial roots of vines (Gill 1969)*

Species	Roots in leaf zone?	Roots association with nodes?	Maximum number per node	Tip Properties			
				Maximum diameter (mm.)	Color	Rigidity and alignment	Laterals without injury?
<i>Rajania cordata</i>	yes	yes	1	0.3	white	flexible, wrinkled	—
<i>Peperomia emarginella</i>	yes	yes	1	0.1	white	bent, flexible delicate	—
<i>Marcgravia sintenisii</i>	yes	yes	4	0.6 (2.0)	cream	unbent, tend to be rigid	—
<i>Gonocalyx portoricensis</i>	yes	yes	5	0.3	white	flexible, crinkled	+
<i>Hornemannia racemosa</i>	yes	yes	1	0.3	white to pale pink to brown	crinkled, flexible	+
<i>Ipomoea repanda</i>	yes	yes	2	0.5	white	weak flexibility, curves	—
<i>Psychotria guadalupensis</i>	yes	yes	4	0.5	cream to light green	flexible, crinkly	+
<i>Mikania pachyphylla</i>	yes	yes	3	0.5	white to pale green	flexible, crinkled	—

Table 70.—*Properties of aerial roots of herbs (Gill 1969)*

Species	Minimum distance leaf zone (cm.)	Roots only at nodes?	Maximum diameter (mm.)	Tip Properties		
				Color	Rigidity and alignment	Laterals without injury
<i>Selaginella krugii</i>	0	branch junctions	0.4	green	flexible but wiry, unbent	—
<i>Isachne angustifolia</i>	0	yes	0.6	white to pale green	straight & flexible	—
<i>Dilomilis montana</i>	2	branch junctions	1.8	green apex, cream behind	corrugated, flexible	—
<i>Pilea obtusata</i>	0	yes	0.3	white to pink	curled, flexible	+
<i>Pilea yunquensis</i>	0	no	0.2	reddish brown	curled, flexible	+
<i>Sauvagesia erecta</i>	0	yes	0.2	pale cream	straight & flexible	—
<i>Begonia decandra</i>	1	yes	0.4	white to tan	straight & flexible	+

Weaver et al. (1973) measured and compared the transpiration rates of species from both the dwarf forest and the tabonuco forest (at La Mina). They obtained values of 0.9–11.4 g/m²·hr for dwarf forest species and 1–16 g/m²·hr for tabonuco forest species. Transpiration rates in dwarf forest were more variable on a day to day basis than were rates in the tabonuco forest. Weaver et al. (1973) also found that under the same environmental conditions (sunny, fog-free periods) thick sclerophyllous leaves of the dwarf forest transpired as much as thinner, membranous leaves of the tabonuco forest. Transpiration

Table 71.—Total epiphyte loads in each working zone at Pico del Este (adapted from Weaver 1972)

Working zone	Total epiphyte load (g/m ²)
Winward	736
Ridge	435
Leeward	475
Mean	549

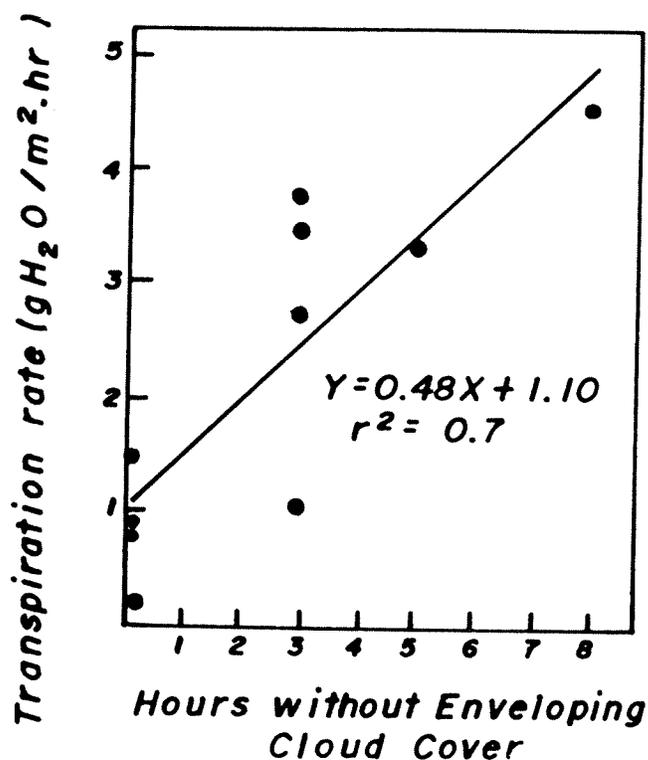


Figure 66.—Relation between mean transpiration rates and number of hours per day without enveloping cloud cover for four tree species at Pico del Este (Weaver 1975).

rates of species with numerous and large stomata were higher than transpiration rates of species with fewer and smaller stomata. This provides evidence that the numerous large stomata are adaptations to increase transpiration rates as suggested by Cintrón (1970). Weaver et al. (1973), as had others earlier (e.g. Odum 1970a), suggested that the dwarfing of vegetation in the cloud shrouded peaks is a result of reduced pumping of minerals by the plants due to low transpiration rates. Because water is not limiting these mountain peaks, Weaver et al. (1973) suggested that the leathery leaves were an adaptation to prevent wind damage. They found that thin leaves from the lower montane forest were soon heavily damaged when placed in the dwarf forest environment.

Phenology.—A large number of plant species in the dwarf forest are in flower during any given month of the year (fig. 67). Annual flowering records for dicots show two peaks; one in July and one in October. The lowest number of dicot species in flower occurred in February. The number of monocots in flower gradually increased to a peak in July, and then decreased to a low in October. The flowering pattern of trees is similar to that of shrubs (fig. 68). With the exception of the small drop in the number of species in flower in May, the flowering pattern for climbers is uniform throughout the year. Two contrasting flowering records were obtained for terrestrial and epiphytic herbs; when epiphytic herbs have a low number of species in flower terrestrial herbs have the maximum number in flower, and vice versa.

Most species of plants in the dwarf forest are insect or bird pollinated (fig. 69). However, Nevling (1971) observed little actual pollination and low percentage of fruit set. He suggested that low fruit set

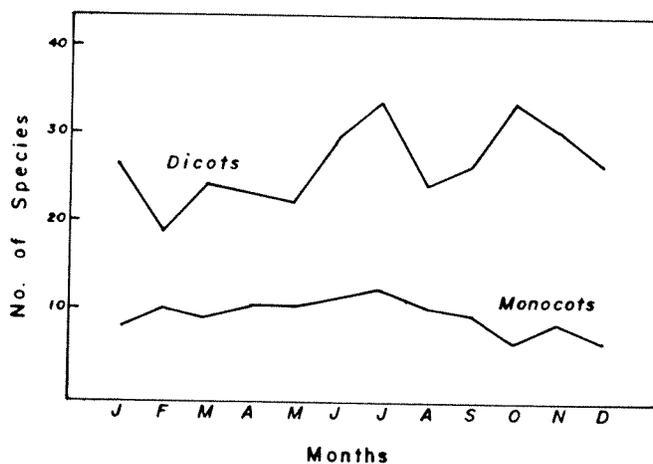


Figure 67.—Cumulative monthly flowering records of the dictoyledons and monocotyledons of Pico del Oeste (Nevling 1971).

Table 72.—Description of trees sampled for mosses (Russell and Miller 1977)

Tree number	Tree species	Height (m)	Dbh (cm)	Number of samples	Number of samples with mosses
1	<i>Eugenia borinquensis</i>	2.5	5	38	31
2	<i>Ocotea spathulata</i>	3.0	5	27	15
3	<i>Calycogonium squamulosum</i>	2.2	1.3	17	10
4	<i>Tabebuia rigida</i>	4.6	20	36	29
5	<i>Calyptranthes krugii</i>	1.9	2.5	12	8
6	<i>Ocotea spathulata</i>	1.2	3.8	8	5
7	<i>Eugenia borinquensis</i>	2.2	5	15	11
8	<i>Ocotea spathulata</i>	1.9	1.3	14	10
9	<i>Calyptranthes krugii</i>	2.2	1.3	15	7
Total				182	126

Table 73.—Distribution of moss species by height on tree* (Russell and Miller 1977)

Tree number Tree species	3 <i>Calycogonium squamulosum</i>			1 <i>Eugenia borinquensis</i>			2 <i>Ocotea spathulata</i>			4 <i>Tabebuia rigida</i>			Average		Total
	2.2			2.5			3.0			4.6			S	D	
Tree height (m)	S	D	N	S	D	N	S	D	N	S	D	N	S	D	N
Height on tree (m)															
0.3	8	5	2	11	2	7	8	2	5	7	6	3	8.50	3.75	17
0.3-1.0	3	4	1	6	4	6	2	0	2	4	1	4	3.75	2.25	13
1.0-1.7	2	1	5	6	5	9	3	0	2	5	1	3	4.00	1.75	19
1.7-2.2	1	0	2	6	1	3	1	0	1	4	5	4	3.00	1.50	10
2.2-2.8				2	0	2	1	3	6	2	7	3	1.67	3.33	11
2.8										3	6	5	3.00	6.00	5
Percentage of tree height															
25	8	5	2	11	2	8	8	2	7	9	3	7	9.00	3.00	24
26-50	3	2	2	6	5	10	3	0	2	6	4	10	4.50	2.75	24
51-75	2	1	4	5	3	4	1	2	3	4	3	6	3.00	2.25	17
76-100	1	0	2	6	2	6	1	6	1	3	6	5	2.75	3.50	14

*The number of species (S), degree of cover (D), and number of collections (N) at each level are indicated.

resulted from high humidity which dilutes the nectar and decreases attractiveness to the pollinators. The number of species requiring wind pollination was low, not surprising since high rainfall in the dwarf forest would place the wind pollinators at a disadvantage because the rain washes the pollen from the air.

Little correlation appears in timing of flowering with climatic variables (fig. 70). A slight tendency for peak flowering in July and October coincides with periods of low rainfall. As a possible adaptation to the adverse conditions for pollination either by wind or by birds and insects, 19 species (approximately 35% of the total) are in flower for more than 10 months of the year, and 42 species (approximately 76% of the total) are in flower for more than 6 months (table 79). These prolonged flowering periods would increase the opportunity for sexual reproduction whenever environmental conditions were suitable.

The annual pattern of monthly fruiting for dicots shows three peaks: one in July coinciding with the peak in flowering, one in March, and one in November (fig. 71). The annual pattern of monthly fruiting for monocots is similar to the pattern of flowering for monocots (c.f. fig. 67). Although fruiting often was initiated, few reached maturity due to bird and insect predation (Nevling 1971).

Succession.—Studies on regrowth of vegetation at three sites (windward, leeward, and summit) in the dwarf forest were made after the sites were clearcut in 1969 (Byer and Weaver 1977). In addition to the clearcut sites, a site severely disturbed by a plane crash in 1968 was also monitored. Ferns and allies and sprout derived woody plants were the dominant life form in both the successional and climax forests (table 80). Plant cover returned quickly after disturbance; 82% cover was attained after three years.

Bryophytes, lichens, algae, and ferns covered most of the area in both the successional and climax forests. The climax dwarf forest had approximately half the number of stems as the successional forest, the difference being mainly due to high stem density of ferns and graminoid species in the successional forest. Mortality of graminoids was high between the second and third year after disturbance; ferns and herbs increased notably during this period. Plant height increased from early successional to climax forest. However, the number of species in the successional forest was almost double the number in the climax forest. The variability of species distribution among series is shown in table 81. The lower number of species in the climax forest is due to the paucity of herb, graminoid, and fern species.

After two years of regrowth the mean biomass of the dwarf forest had only increased to 190 g/m². However, during the next four years biomass increased five-fold (table 82). Biomass at the summit site exceeded biomass at either the windward or leeward sites. Biomass of sprouting vegetation at the summit site was higher than nonsprouting vegetation; however, biomass of sprouting vegetation at the

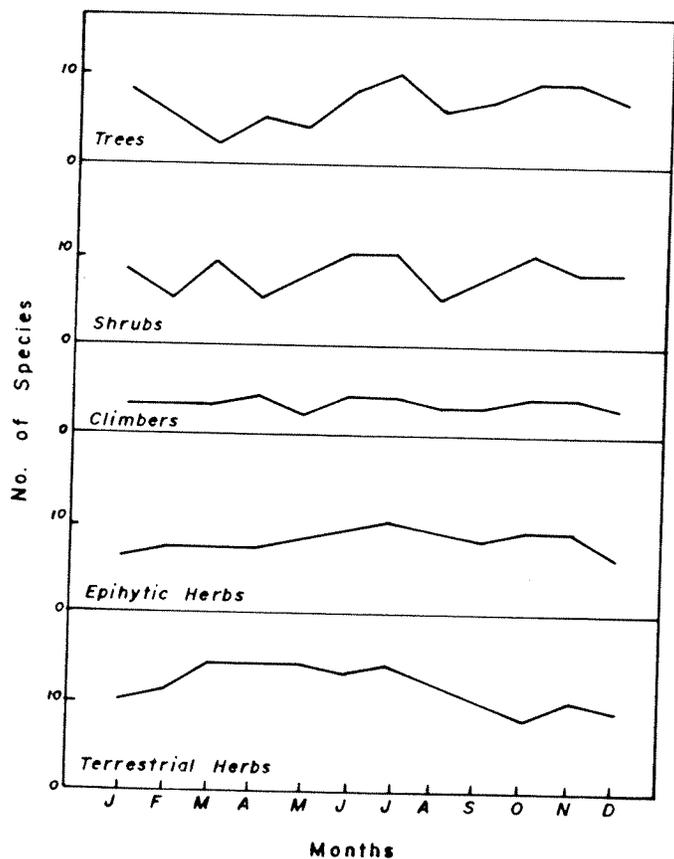


Figure 68.—Cumulative monthly flowering records of plants, divided according to life form, at Pico del Oeste (Neuling 1971).

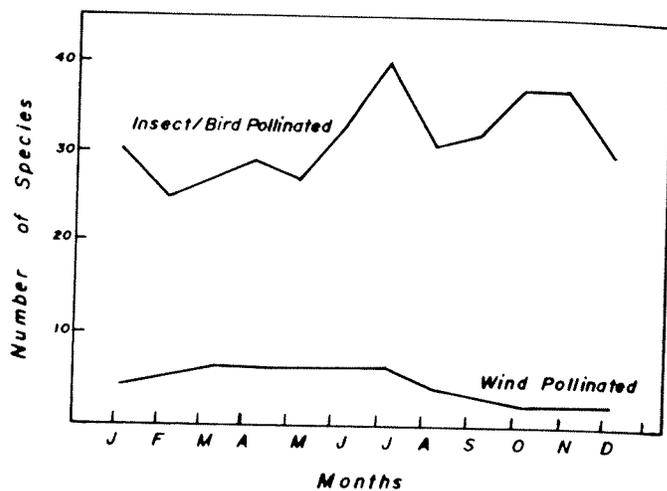


Figure 69.—Cumulative monthly flowering records from Pico del Oeste plotted as species with insect/bird pollination syndrome vs. species with wind pollination syndrome (Neuling 1971).

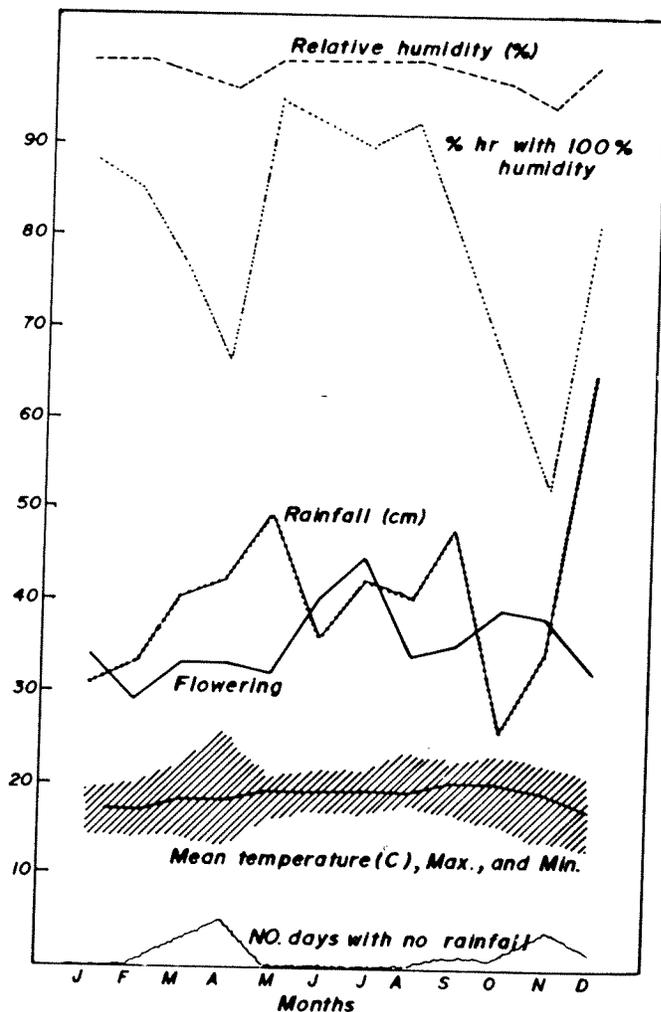


Figure 70.—Flowering data of Pico del Oeste correlated with climatic data (Neuling 1971).

Table 74.—Distribution of moss species by tree* (Russell and Miller 1977)

Tree number	3		5		9		1		7		2		6		8		4		P
	<i>Colycogonium squamulosum</i>		<i>Calypttranthes krugii</i>		<i>Calypttranthes krugii</i>		<i>Eugenia borinquensis</i>		<i>Eugenia borinquensis</i>		<i>Ocotea spathulata</i>		<i>Ocotea spathulata</i>		<i>Ocotea spathulata</i>		<i>Tabebuia rigida</i>		
	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	
<i>Acroporium acestrostegium</i>											0	13							11
<i>Acroporium pungens</i>	1	50	1	88	0	43	2	87	9	73	0	60	1	60	1	70	0	60	100
<i>Callicostella depressa</i>											0	13	0	20			0	4	56
<i>Campylopus cygneus</i>			0	25			0	16			0	13	0	20			0	4	56
<i>Hemiragis aurea</i>	6	10	1	25	1	43	0	19			1	27	0	20	1	30	2	14	89
<i>Hookeriopsis acicularis</i>	0	10					0	6	0	9							0	4	22
<i>Hookeriopsis obsoletinervis</i>							0	13									0	7	33
<i>Hypnella filiformis</i>							0	6			0	7					0	7	33
<i>Isodrepanium lentulum</i>							0	3											11
<i>Lepyrodontopsis trichophylla</i>					0	14													22
<i>Leucobryum martianum</i>	0	10					0	23			0	20	4	20			0	4	67
<i>Leucoloma serrulatum</i>	1	10	2	25			0	3									1	21	22
<i>Macromitrium perichaetiale</i>					3	14	0	10	3	9							1	25	44
<i>Macromitrium schwaneckeanum</i>									0	18							0	4	22
<i>Micromitrium scoparium</i>	0	100	2	50	0	43	2	30	2	82	1	73	2	100	3	50	3	71	100
<i>Syrrhopodon prolifer</i>	0	20	0	12	2	29	0	58	0	45	0	20							67
<i>Thuidium urceolatum</i>	0	20	0	12							0	7					0	7	44
<i>Vesicularia</i> sp.							0	3											11
Number of species	8		7		6		13		6		9		5		3		12		

*The degree of cover (D), constancy (C), and presence (P) are indicated for each moss species. D=0 = trace; D=1 = 11–20%; etc.

Table 75.—Distribution of moss species on leeward and windward sides of trees* (Russell and Miller 1977)

Growth-form	Number of collections	Leeward (10)		Windward (13)	
		D	C	D	C
Te	<i>Acroporium pungens</i>	0	90	1	77
W	<i>Callicostella depressa</i>	0	10	0	8
Te	<i>Campylopus cygneus</i>	0	10		
W	<i>Hemiragis aurea</i>	0	10	0	8
W	<i>Hookeriopsis acicularis</i>			0	8
W	<i>Hookeriopsis obsoletinervis</i>			0	15
W	<i>Hypnella filiformis</i>	0	10	0	8
Cu	<i>Leucobryum martianum</i>			0	15
Te	<i>Leucoloma serrulatum</i>	2	30	0	15
To	<i>Macromitrium perichaetiale</i>	0	10	1	15
To	<i>Macromitrium schwaneckeanum</i>	0	10	0	8
To	<i>Macromitrium scoparium</i>	0	60	0	46
t	<i>Syrrhopodon prolifer</i>	0	20	0	23
W	<i>Thuidium urceolatum</i>	0	10		
	Number of species		11		12

*Growth-form, degree of cover (D), and constancy (C) are indicated.

other two sites was a minor component of their total biomass. Biomass accumulation during the first two years after clearing was 95 g/m²·yr; during the next four years, average biomass accumulation increased approximately two-fold to 212 g/m²·yr. Recovery of the dwarf forest is slow after disturbance as slow height increase and low biomass accumulation show.

Long-term Observations of Forest Dynamics

Permanent plots (0.2 or 0.4 ha) in several forest types in the Luquillo Experimental Forest have been measured at various intervals for approximately 30 yr by the U.S. Forest Service. The location of the plots and their descriptions are given in figure 72 and table 83, respectively. Each tree in every plot is permanently marked for reidentification and repeated measurement.

A summary of the changes in stem density, basal area, and mortality during the first 5-yr period after the plots were established is given in table 84. Mortality rates were similar for both virgin tabonuco and colorado forests, regardless of location. Ingrowth (the number of new stems present between measurement periods) was not included because no trees entered the 5 cm class. Changes in basal area were positive in the tabonuco forest, but mean changes in the two types of colorado forests were negative. Therefore, for the 5-yr period, the tabonuco forest had a net gain in organic matter, but the colorado forest had a net loss of organic matter.

Different trends in forest dynamics are revealed when changes are measured over long time periods, such as approximately 30 yr (table 85). Mortality rate in the virgin colorado forest (plots CV-1 and 3 and CS-2 and 4) was approximately 18 stems/ha·yr lower than the approximately 26 stems/ha·yr in virgin tabonuco and palm forests (plots TS-2 and 3,

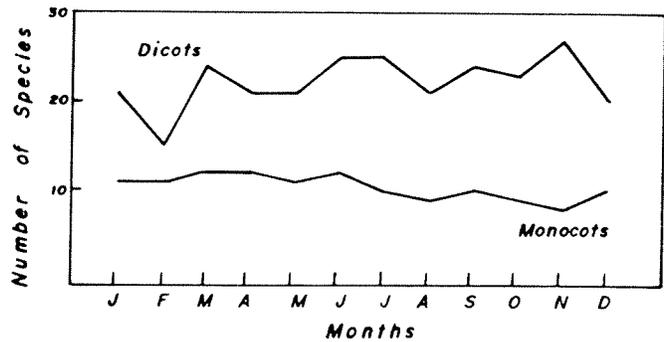


Figure 71.—Cumulative monthly fruiting records of species of dicotyledons and monocotyledons at Pico del Oeste (Neuling 1971).

TR-1, and PV-2). Also, ingrowth in the virgin colorado forest (approximately 25 stems/ha·yr) was higher than that in virgin tabonuco and palm forests (approximately 13 stems/ha·yr), resulting in a net addition of stems to the colorado forest and a net loss from the tabonuco and palm forests.

Changes in basal area of virgin tabonuco and colorado forests were similar (1,565 cm²/ha·yr and 1,172 cm²/ha·yr, respectively). No net growth in the palm forest was measured, and, in fact, the basal area decreased slightly over the 29-yr period.

Although it has been proposed that the virgin colorado forest is slow growing with little production (Tropical Forest Experiment Station 1952), over a 30-yr period the average basal area increment was similar to that of the virgin tabonuco forest. However, because the tabonuco forest is taller and biomass is a function of both diameter and height, absolute wood biomass production in the tabonuco forest was probably greater than in the colorado forest.

Two plots in both the tabonuco and colorado forest (TCU-1 and 2 and CCU-1 and 2) were partially cut in 1947, reducing the basal area by about 50%. All trees with a dbh ≥ 50 cm were cut and removed. After five years, ingrowth in the tabonuco forest (128 stems/ha·yr) was approximately five times higher than in the colorado forest (26 stems/ha·yr; table 85). Average basal area increment in the tabonuco forest was approximately 15,000 cm²/ha·yr, whereas in the colorado forest the mean for the two plots was approximately zero. Mean basal area increments when adjusted for mortality may be translated into volume increments of 7.7 m³/ha·yr and 0.6 m³/ha·yr for the tabonuco and colorado forests, respectively (Tropical Forest Experiment Station 1953). In 1958, the cutover colorado plots were observed again. At this time no spectacular response was noticed; the forest was as open as when first cut, no new seedlings were observed, and open areas were covered with dense stands of razor grass (*Scleria* sp.)

Table 76.—Insect damage to plants in the dwarf forest at Pico del Oeste (Howard 1969)

Plant species	Percent damaged	Percent reduction in surface area
<i>Clusia grisebachiana</i>	98	24
<i>Haenianthus salicifolia</i>	86	19
<i>Wallenia yunquensis</i>	84	16
<i>Eugenia borinquensis</i>	81	25
<i>Miconia foveolata</i>	81	35
<i>Miconia pachyphylla</i>	79	21
<i>Grammadenia sintenisii</i>	77
<i>Hornemannia racemosa</i>	73
<i>Rajania cordata</i>	70
<i>Peperomia hernandiifolia</i>	70

Table 77.—Mean transpiration rates of typical dwarf forest species in sun and shade conditions at Pico del Este. Units are g H₂O/m²·hr (Weaver 1975)

Run	Date	Exposure	Successional*		Climax*		Exposure mean	Day mean
			CE	PR	OS	TR		
1	1/5/72	sun	1.52	0.89	0.87	1.50	1.20	1.04
		shade	0.91	1.46	0.56	0.60	0.88	
	1/6/72	sun	4.54	6.77	6.41	3.02	5.19	4.67
		shade	4.35	5.77	3.97	2.50	4.25	
2	1/22/72	sun	8.24	1.76	5.00	3.35
		shade	1.50	1.90	1.70	
	1/23/72	sun	5.83	1.73	3.78	2.77
		shade	2.00	1.52	1.76	
3	3/4/72	sun	6.83	4.52	5.68	3.84
		shade	1.60	2.39	2.00	
	3/5/72	sun	6.30	6.74	6.52	3.51
		shade	0.59	0.41	0.50	
4	3/23/72	sun	2.24	1.49	1.58	1.11	1.60	1.60
		shade	
	3/24/72	sun	1.00	1.02	0.81	1.06	0.97	0.97
		shade	
5	4/15/72	sun	0.97
		shade	1.49	1.26	0.51	0.64	0.97	
	4/16/72	sun	0.23
		shade	0.37	0.46	0.00	0.09	0.23	
Exposure means		sun	3.88	4.04	3.40	1.58	3.23	
		shade	1.34	1.77	1.11	1.19	1.36	
Grand species means			2.62	2.91	2.26	1.39		2.30

*CE = *Clibadium erosum*, PR = *Palicourea riparia*, OS = *Ocotea spathulata*, TR = *Tabebuia rigida*.

(Tropical Forest Research Center 1958). However, by 1975, 18 yr later, dramatic changes had taken place in these plots (table 85). (Because plots TCU-1 and CCU-1 were not monitored beyond 1952 this discussion will be restricted to a comparison between plots TCU-2 and CCU-2). Over the 28-yr period average mortality in the tabonuco forest was twice as high as in the colorado forest whereas ingrowth was approximately twice as high in the colorado as in the tabonuco. More stems were added to the colorado forest than to the tabonuco forest. Basal area increment during the first 5-yr period was 8 times higher in the tabonuco than in the colorado, but averaged over 28 yr, the basal area increment in the tabonuco forest was only 1.5 times higher. These results suggest that the tabonuco forest recovers quickly from the stress of cutting, whereas the colorado forest is initially slower to recover, but given sufficient time, its recovery rate is eventually as fast as that of the tabonuco forest. Both disturbed forest still have higher annual basal area increments and ingrowth rates than those in their corresponding virgin forests.

Crow (1980) analyzed the 30 years of records for the El Verde plots 2 and 3. He found that structural components of the forest had two phases of development during this period. During the first phase, stem density increased (fig. 73a) and basal area (fig. 73c)

Table 78.—Range of transpiration rates of dwarf forest species at Pico del Este. Units are g H₂O/m²·hr (Weaver 1975)

Species	Sun	Shade
<i>Clibadium erosum</i>	0.30– 9.24	0.22–5.20
<i>Palicourea riparia</i>	0.47–12.35	0.41–6.54
<i>Ocotea spathulata</i>	0.60– 8.96	0.00–5.54
<i>Tabebuia rigida</i>	0.00– 3.55	0.00–3.37

Table 79.—Length of flowering period for species in the dwarf forest at Pico del Oeste (Neuling 1971)

No. months in flower	No. of species	% of species in flower in July	% of species in flower in October
12	10	100	100
11	7	100	100
10	2	100	100
9	7	100	85
8	5	100	80
7	6	100	50
6	5	60	40
5	2	50	100
4	3	66	33
3	2	50	50
2	1	100	100
1	1	0	0
0	4	0	0

Table 80.—Summary of several parameters for 10 life form categories in the dwarf forest at Pico del Este. Values are the means \pm 1S.E. (from Byer and Weaver 1977)

Life form	% frequency ^a			Density/1000 m ²			% Cover		
	1971	1972	Climax	1971	1972	Climax	1971	1972	Climax
Bryo-lichen-alga	33.59 \pm 3.24	33.50 \pm 2.82	47.80 \pm 8.19
Clasping	13	33	70	133 \pm 44	568 \pm 151	3,300 \pm 1,260	0.30 \pm 0.28	0.10 \pm 0.05	1.38 \pm 0.44
Epiphytes	52	57	70	3,883 \pm 1,009	3,000 \pm 700	8,500 \pm 3,910	0.31 \pm 0.08	0.56 \pm 0.13	4.22 \pm 1.52
Fern & Allies	100	100	90	26,617 \pm 2,360	52,627 \pm 5,274	11,800 \pm 3,540	10.41 \pm 1.15	13.75 \pm 1.17	35.60 \pm 17.63
Gramminoid	87	94	50	21,967 \pm 4,698	16,039 \pm 1,565	2,500 \pm 1,340	7.34 \pm 1.36	19.14 \pm 2.79	1.06 \pm 0.43
Herb	7	27	83 \pm 42	3,353 \pm 981	0.04 \pm 0.02	0.62 \pm 0.28
Palm	3	3	10	83 \pm 49	78 \pm 46	200 \pm 200	0.02 \pm 0.00	0.02 \pm 0.01	0.04 \pm 0.04
Seedling, woody ^d	55	47	100	3,683 \pm 1,935	2,431 \pm 785	2,500 \pm 1,035	2.89 \pm 0.82	1.84 \pm 0.52	1.27 \pm 1.08
Sprout, woody ^d	96	96	100	13,867 \pm 1,917	12,725 \pm 2,209	11,700 \pm 1,653	5.84 \pm 1.10	12.21 \pm 2.33	21.96 \pm 14.90
Vine	22	27	10	433 \pm 122	627 \pm 188	100 \pm 100	0.26 \pm 0.08	0.25 \pm 0.10	0.03 \pm 0.03
Total	70,749 \pm 6,028	91,448 \pm 4,903	40,600 \pm 7,954	61.00 \pm 3.54	81.99 \pm 3.75	113.36 \pm 19.62

Life form	Mean of maximum heights ^b cm.			No. species ^c			
	1971	1972	Climax	1971	1972	Climax	Plane wreck
Bryo-lichen alga	1	2
Clasping	2	1	2	1
Epiphytes	4.2 \pm 1.0	16.1 \pm 3.4	21.2 \pm 6.2	3	3	4	3
Fern & Allies	22.0 \pm 1.4	39.8 \pm 3.7	35.6 \pm 17.6	17	23	6	21
Gramminoid	33.7 \pm 3.2	50.0 \pm 3.8	35.5 \pm 14.9	7	6	2	8
Herb	0.7 \pm 0.4	4.5 \pm 1.2	2	2	2
Palm	0.5 \pm 0.3	0.6 \pm 0.4	1.2 \pm 1.2	1	1	1	1
Seedling, woody ^d	20.5 \pm 4.4	39.4 \pm 7.7	24.3 \pm 15.2	24	8	8	12
Sprout, woody ^d	33.6 \pm 4.2	68.6 \pm 8.1	101.5 \pm 17.0	8	8	5	7
Vine	2	3	1	5
Total	66	54	30	62

^aIn 1 \times 1 quadrats.

^bMean of tallest plant in each quadrat.

^cBryo-lichen-alga species not included in totals.

^dIncludes all species derived from this type of reproduction at the clearcut sites.

and biomass (fig. 73d) rapidly increased. Species diversity (fig. 73e), as measured by the Shannon Diversity Index, increased early corresponding with the early gain in new species (fig. 73b). The second phase was characterized by a decline in stem density, species diversity, and new species entrance. At the end of the 30-yr period, these forest components had not reached steady state. The downward trend in species diversity conflicts with the general hypothesis that diversity increases with maturity. Increases in basal area and biomass slowed down to almost steady state conditions of 25 m²/ha and 265 t/ha, respectively.

The increase in stem density between 1943 and 1946 was due to a surge of ingrowth; 216 stems entered the 4–8 cm class during this period. The number of trees in the larger diameter classes remained relatively constant, e.g. the number of trees greater than 32 cm dbh increased from 60 in 1943 to 67 in 1976.

Tree height distribution in the forest also changed over time (fig. 74). In 1946 few trees were taller than 18 m, and most were 6–12 m tall. However, in 1976,

although some trees were as tall as 33–36 m, the majority were still 6–12 m tall.

Crow (1980) hypothesized that the changes in stand characteristics measured in the 1940's and 1950's represented forest response to a hurricane in 1932. If this were the case, then based on the results of Crow's study, it takes approximately 40 yr for the tabonuco forest to recover structurally from a severe natural disturbance.

In addition to the permanent plots, Crow and Weaver (1977) observed long-term (18 yr) changes in three other areas of the Luquillo Experimental Forest. These plots were located in the tabonuco forest on similar soil types at different elevations (from 180–600 m), and on different slopes. The three areas were: Río Grande located in the western part of the Forest, Sabana 4, and Sabana 8, both located in the northeastern part of the Forest. The Río Grande and Sabana 8 plots were lightly thinned in 1957. All plots were initially measured in 1957 and remeasured in 1975. No significant differences were obtained in either the mean diameter increment of all species

Table 81.—Percent cover of all species in various sites in the dwarf forest at Pico del Este. The symbol "T" indicates trace, i.e. less than 0.01% cover (Byer and Weaver 1977)

Life form category and species	Site			
	1971	1972	Elfin woodland	Plane wreck
Bryo-lichen-alga				
alga	0.22	0.62
lichen	0.02	0.04
<i>Marchantia</i> sp.	T
moss	28.83	33.82	49.80	3.00
Clasping				
<i>Marcgravia rectiflora</i> Tr. & Pl.	T	0.21
<i>Marcgravia sintenisii</i> Urban	0.30	0.09	1.17	0.05
Epiphyte				
<i>Anthurium dominicense</i> Schott	0.60
<i>Brachynidium parvum</i> Cogn.	0.01
<i>Gonocalyx portoricensis</i> (Urb.) A. C. Smith	0.01	T
<i>Guzmania berteroniana</i> (R. & S.) Mez.	3.29
<i>Dilomilis montana</i> (Sw.) Summerhayes	0.25	0.50	0.69	0.05
<i>Vriesia sintenisii</i> (Baker) Sm. & Pitt.	0.05	0.09	0.18	T
Fern & allies				
<i>Cyathea borinquena</i> (Maxon) Domin	0.70	1.64	0.30	3.00
<i>Lophosoria quadripinnata</i> (Geml.)	0.05
<i>Cyathea arborea</i> (L.) J. E. Smith	3.00
<i>Alsophila bryophila</i> Tryon	2.70	2.80	3.37	17.50
<i>Dennstaedtia</i> sp.	0.17
<i>Diplazium l'herminieri</i> Hieron.	0.04	0.18
<i>Thelypteris dentata</i> (Forsk.) E. St. John	T
<i>Thelypteris reticulata</i> (L.) Proctor	T
<i>Ctenitis subincisa</i> (Willd.) Copel.	0.22	0.01	T
<i>Hemidictyum marginatum</i> (L.) Presl.	T
<i>Gleichenia bifida</i> (Willd.) Spreng.	0.10	0.13	T
<i>Lycopodium cernuum</i> L.	0.18	2.71	3.00
<i>Nephrolepis rivularis</i> (Vahl.) Mett.	0.05
<i>Odontosoria aculeata</i> (L.) J. Smith	1.04	0.13	0.05
<i>Odontosoria uncinella</i> (Kunze) Fée	1.35	0.28	T
<i>Pityrogramma calomelanos</i> (L.) Link	0.10
<i>Polypodium crassifolium</i> L.	T
<i>Grammitis serrulata</i> (Sw.) Sw.	T
<i>Polypodium loriceum</i> L.	0.01	0.05
<i>Polypodium lycopodioides</i> L.	0.03
<i>Selaginella krugii</i> Hieron.	0.43	0.51	3.82	3.00
<i>Blechnum lineatum</i> (Sw.) C. Chr.	2.65	4.43	0.18	0.50
<i>Trichomanes rigidum</i> Sw.	T	T	0.10
unidentified (13)	0.18	0.24	T
Gramminoid				
<i>Andropogon bicornis</i> L.	0.20	0.11	3.00
<i>Carex polystachya</i> Sw.	T	3.00
<i>Eleocharis</i> sp.	T
<i>Ichnanthus pallens</i> (Sw.) Munro	0.05
<i>Isachne angustifolia</i> Nash	6.95	17.52	0.80	25.00
<i>Paspalum conjugatum</i> Berg.	0.05
<i>Rynchospora cyperoides</i> (Sw.) Mart.	T
<i>Scleria canescens</i> Boeckl.	1.08	4.35	0.98
unidentified (5)	0.01	0.02
Herb				
<i>Desmodium</i> sp.	0.03	T
<i>Elephantopus scaber</i> L.	T
<i>Erechtites hieracifolia</i> (L.) Raf.	T
<i>Justicia verticillaris</i> (Nees) Urban	0.01	0.44
<i>Sauvagesia erecta</i> L.	0.80
Palm				
<i>Prestoea montana</i> (R. Grah.) Nichols.	0.02	0.02	3.33	T

Table 81.—Percent cover of all species in various sites in the dwarf forest at Pico del Este. The Symbol "T" indicates trace, i.e. less than 0.01% cover (Byer and Weaver 1977)—Continued

Life form category and species	Site			
	1971	1972	Elfin woodland	Plane wreck
Seedling, woody				
<i>Cecropia peltata</i> L.	0.04	0.10
<i>Clibadium erosum</i> (Sw.) DC	1.97	0.65	0.05
<i>Clusia</i> sp.	T	0.02	0.06	T
Compositae unidentified	T
<i>Ficus citrifolia</i> P. Mill.	T
<i>Lobelia portoricensis</i> (Vatke) Urban	T
<i>Miconia pachyphylla</i> Cogn.	0.12	T
<i>Miconia pycnoneura</i> Urban	T
<i>Miconia sintenisii</i> Cogn.	T	0.07	0.90
<i>Piptocarpha tetrantha</i> Urban	T
<i>Psychotria berteriana</i> DC	0.73	1.36	0.15	3.00
<i>Psychotria grosourdyana</i> (Baill.) Urban	0.04	0.04	0.02	T
<i>Rubus rosaefolius</i> Smith	T
<i>Tabebuia heterophylla</i> (DC) Britton	0.03	0.07
unidentified (21)	0.11	T	0.20
Sprout, woody				
<i>Ardisia obovata</i> Desv.	0.09	0.05	T
<i>Calycogonium squamulosum</i> Cogn. ^a	0.10	0.08	2.76	0.05
<i>Calyptranthes krugii</i> Kiaersk	0.18	0.43	0.90	0.05
<i>Eugenia borinquensis</i> Britton	3.31	7.45	0.31	3.00
<i>Micropholis garcinifolia</i> Pierre ^a	0.06	0.06	T
<i>Ocotea spathulata</i> Mez. ^a	1.12	1.96	16.89	3.00
<i>Tabebuia rigida</i> Urban ^a	1.06	1.69	0.06	0.50
<i>Walienia yunquensis</i> (Urb.) Mez.	0.19	0.30	0.79	0.05
Vine				
<i>Alloplectus ambiguus</i> Urban	0.30	T
<i>Ipomoea repanda</i> Jacq.	0.10	0.04
<i>Mikania cordifolia</i> (L. f.) Willd.	T
<i>Mikania fragilis</i> Urban	T
<i>Mikania pachyphylla</i> Urban	0.29	T
<i>Rajania cordata</i> L.	0.16	0.19	T

^aSpecies significantly clumped at first reading, but not second.

Table 82.—Mean above ground biomass change for three clearcut sites in the dwarf forest at Pico del Este (Byer and Weaver 1977)

Site	Three plot mean, 1971			Three plot mean, 1975		
	Sprout	(g/m ²) non-sprout	Total	Sprout	(g/m ²) non-sprout	Total
Windward	14	57	71	39	404	443
Summit	215	191	406	1117	510	1627
Leeward	20	74	94	207	835	1041
Mean of three sites	83	107	190	454	583	1037
Yearly biomass accumulation	41	53	95	76	97	173

(0.43–0.52 cm/yr; table 86) or the mean area increment of all species (16.8–19.0 cm²/yr; table 87). Lightly thinning the tabonuco forest did not, therefore, enhance the production of individual trees in the forest. For most species, mean diameter growth rates were constant regardless of the diameter of the trees (fig. 75). Only *Tabebuia*, *Ocotea*, and *Alchornea* showed increases in diameter growth with increasing diameter. The authors concluded that the growth rates of these forests were low, and that perhaps wet tropical forests were not as productive as previously reported. However, changes in diameter and basal area per tree are not a measure of productivity; the total density of the stand and its height should also be considered.

Plantations

Between 1933 and 1945 over 2,326 ha of plantations, representing dozens of species, were planted within the Forest, on a wide variety of sites. Marrero (1947) summarized growth performance of species tested in these plantings (table 88). Over 4 million seedlings and over 20 thousand kg seeds were planted. More exotic species were planted than native species. Native species generally had higher survival and higher growth rates than did exotic species. Between 1959–61, several dozen additional species were tested in single-tree-plot adaptability trials at three locations. These trials were part of a much larger island-wide assessment of potential commercial species (Geary and Briscoe 1972). An arboretum near El Verde, initially started in 1960, now has over 100 species planted in it.

More recent studies have concentrated on identifying provenances of mahogany (*Swietenia* sp; Geary et al. 1973), teak (*Tectona grandis*), and pines (*Pinus caribaea* and *P. oocarpa*) that are adapted to soil and climatic variation within the Luquillo Experimental Forest. The oldest mahogany planting is

almost 50 years old and has been thinned three times. In the newer mahogany trials, 20 seed sources were planted into a gene bank near El Verde in 1964–65; some of these sources no longer exist in their native ranges due to uncontrolled exploitation of natural stands. Since the early 1970's several hundred hectares have been planted to mahogany as part of a continuous National Forest Program to improve certain areas of existing natural forest.

Although *Pinus merkusii* did not perform well in the Luquillo Experimental Forest (Whitmore 1972), certain provenances of *P. caribaea* and *P. oocarpa* have grown very well in 5- and 6-year-old trials. Overall growth performance data are now being analyzed for all provenances of both species and readied for publication. These trials are an international cooperative effort with the Commonwealth Forestry Institute at Oxford University in Great Britain and over 40 countries constituting a part of a world-wide assessment of commercial value of the two species. Counting provenance, spacing, demonstration plantings, within the forest there are about 40 ha of pine plantations which range from 6 to 20 years in age.

FAUNA

Despite frequent reference to the high faunal diversity of tropical rain forests, total animal biomass, estimated to be less than 12 g/m² in the tabonuco forest (Odum 1970b), is less than one tenth that of a tropical coral reef, and ecosystem with similar high productivity (Lugo et al. 1974). Tables 89 and 90 illustrate distribution of animal biomass among taxonomic groups and trophic levels (Odum 1970b; Odum et al. 1970). Total biomass of herbivores was approximately 15 times higher than total biomass of carnivores. Approximately half of the animal biomass in the tabonuco forest is found above the litter layer; however, the most important group weight are earthworms, accounting for 36% of the total.

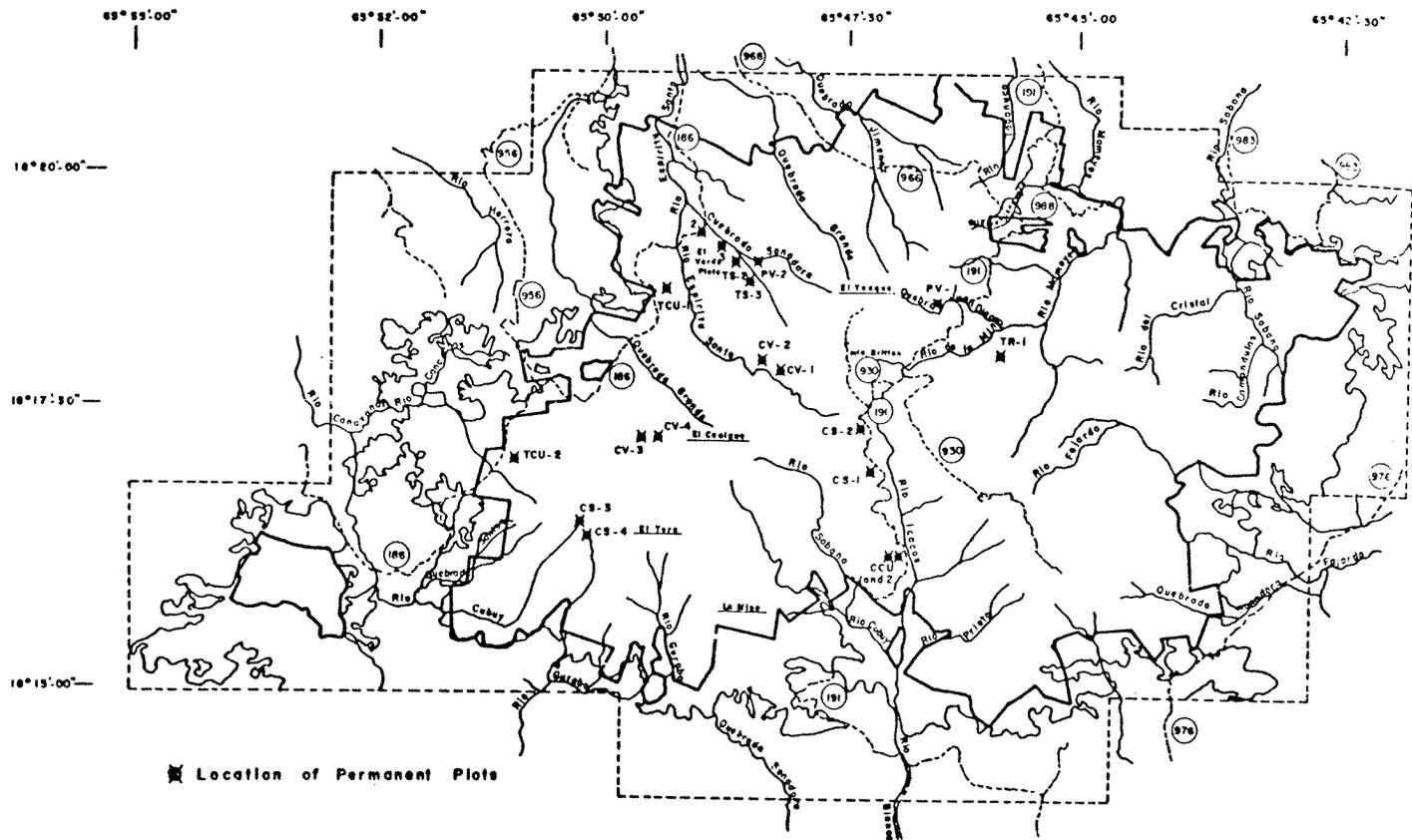


Figure 72.—Location of permanent forest plots in the Luquillo Experimental Forest.

Insects

Taxonomic descriptions of the insects of Puerto Rico have been produced by Martorell (1945) and Wolcott (1948) and specific taxons dealt with by Curran (1928) for Diptera, Forbes (1930) and Schauss (1940) for moths, Klots (1932) for Odonata, Osborn (1935) for Homoptera, Barbour (1939) for Hemiptera-Heteroptera, Petrunkevitch (1929-1930) for spiders, and Comstock (1944) for Lepidoptera. Wolcott (1948) in particular has classified the forest insects of Puerto Rico according to the plants upon which they are known to feed. Both Wolcott (1948) and Drewry (1970a) have reported high insect diversity, in the absence of large numbers, relative to that found in temperate forests. McMahan and Sollins (1970) reported high diversity of litter microarthropods at El Verde (table 91). Omitting larvae and nymphs, 3,872 individuals of 313 species were collected, resulting in a diversity index of 81 species/1,000 individuals. Over 60% of the specimens were represented by only 8% of the species. Collections at El Verde yielded 1,200 species in 183 families and 18 orders (Drewry 1970a). Specimens are presently catalogued and maintained at the El Verde Field Station.

Allan et al. (1973) studied arthropod communities in foliage of secondary vegetation at five sites in Puerto Rico, including El Verde, and compared them with those of other Caribbean islands and the Central American mainland. Species diversity was similar to that of a temperate woods and significantly lower than that of mainland Central America. Insect abundance in the Puerto Rican sites was also less than that on the continent. However, the proportion of predators, primarily spiders, was greater in the Puerto Rican samples than on the mainland. Allan et al. (1973) suggested that this may be explained in part by decreased competition from the predation by the fewer species and lesser abundance of birds in Puerto Rico. The role of the abundant insectivorous anoline lizard remains to be investigated.

Catch of mosquitoes in the El Verde area showed a distinct seasonal phenomena with the highest catch during October and November (fig. 76). It was suggested that this increase in catch was due to the decrease in winter temperatures (Weinbren and Weinbren 1970).

Two species of termites found in the tabonuco forest and the effects of irradiation on them were examined by McMahan (1970). Energetics, censuses, and life

Table 83.—Permanent plots^a in the Luquillo Experimental Forest

Plot ^b	Topography	Vegetation type	Period of study	Condition of forest at start of study
CV-1	Valley	1945-1976	Colorado	Virgin
CV-2	Valley	1945-1951	Colorado	Virgin
CV-3	Valley	1945-1976	Colorado	Virgin
CV-4	Valley	1945-1951	Colorado	Virgin
CS-1	Slope	1945-1963	Colorado	Virgin
CS-2	Slope	1945-1976	Colorado	Virgin
CS-3	Slope	1945-1951	Colorado	Virgin
CS-4	Slope	1945-1976	Colorado	Virgin
CCU-1	1947-1975	Colorado	50% reduction in basal area.
CCU-2	1947-1976	Colorado	50% reduction in basal area.
PV-1	Valley	1946-1951	Palm	Virgin
PV-2	Valley	1946-1976	Palm	Virgin
TR-1	Ridge	1946-1976	Tabonuco	Virgin
TS-2	Slope	1940-1975	Tabonuco	Lightly cut 1917.
TS-3	Slope	1945-1976	Tabonuco	Virgin
TCU-1	1947-1952	Tabonuco	50% reduction in basal area.
TCU-2	1947-1975	Tabonuco	50% reduction in basal area.
El Verde #2		1943-1975	Tabonuco
El Verde #3		1943-1975	Tabonuco

^aPlot size is 0.4 ha, with the exception of CCU-1, CCU-2, TCU-1, and TCU-2 which are 0.2 ha.

^bC = Colorado T = Tabonuco P = Palm V = Valley S = Slope R = Ridge
CU = Cut

Table 84.—Changes in stem density, basal area, and mortality (trees dbh > 5 cm) of virgin tabonuco and colorado forest plots after a 5-yr period (adapted from Tropical Forest Experiment Station 1952)

Plot ^a	Forest	Stem density (no./ha)		Mortality (no./ha·yr)	Basal area (m ² /ha)		Change in basal area (m ² /ha·yr)
		1945	1950		1945	1950	
TR-1	Tabonuco	1,762	1,576	37	43.8	46.6	+0.56
TS-3	Tabonuco	2,340	2,100	48	41.6	42.9	+0.26
CS-1	Colorado	2,236	2,108	26	45.7	45.9	+0.04
CS-2	Colorado	1,796	1,668	26	38.8	38.8	0.0
CS-3	Colorado	1,673	1,384	58	47.5	45.7	-0.36
CS-4	Colorado	1,809	1,702	21	53.7	53.0	-0.14
Mean ^b		1,879	1,716	33	46.4	45.9	-0.12
		(123)	(149)	(8)	(3.1)	(2.9)	(0.10)
CV-1	Colorado	1,633	1,475	32	35.8	34.2	-0.32
CV-2	Colorado	1,450	1,156	59	23.9	24.6	+0.14
CV-3	Colorado	1,947	1,814	27	44.5	43.4	-0.22
CV-4	Colorado	1,989	1,880	22	34.2	35.1	+0.18
Mean ^b		1,755	1,581	35	34.6	34.3	-0.06
		(129)	(167)	(8)	(4.2)	(3.8)	(0.12)

^aT = Tabonuco C = Colorado S = Slope R = Ridge V = Valley

^b1 standard error is given in parenthesis.

Table 85.—Summary of forest dynamics (based on trees with dbh ≥ 4.0 cm) in the Luquillo Experimental Forest (adapted from Tropical Forest Experiment Station 1953; Weaver 1979 and 1980)

Plot ^a	Forest	Final basal area (m ² /ha)	Change in basal area (cm ² /ha·yr)	Final stem density (no/ha)	Mortality (no/ha·yr)	In growth (no/ha·yr)	Years of observation (yr)
TS-2&3	Tabonuco	43.5	663	2,035	32	21	1946–76
TR-1	Tabonuco	51.1	2,467	1,188	24	5	1946–76
TCU-1 ^b	Tabonuco	14,000	147	1947–52
TCU-2 ^b	Tabonuco	16,000	109	1947–52
TCU-2	Tabonuco	33.3	6,339	2,175	37	27	1947–75
PV-2	Palm	31.8	–34	1,470	22	12	1946–75
CV-1 ^b	Colorado	42.9	2,317	1,873	20	27	1946–76
CV-3	Colorado	45.8	467	2,242	19	28	1946–76
CS-2&4	Colorado	41.0	733	1,871	17	19	1946–76
CCU-1 ^b	Colorado	–2,000	1947–52
CCU-2 ^b	Colorado	2,000	26	1947–52
CCU-2	Colorado	34.4	4,321	3,250	16	59	1947–1975

^aT = Tabonuco P = Palm C = Colorado S = Slope R = Ridge V = Valley CU = Cut
^bBased on trees dbh ≥ 5 cm.

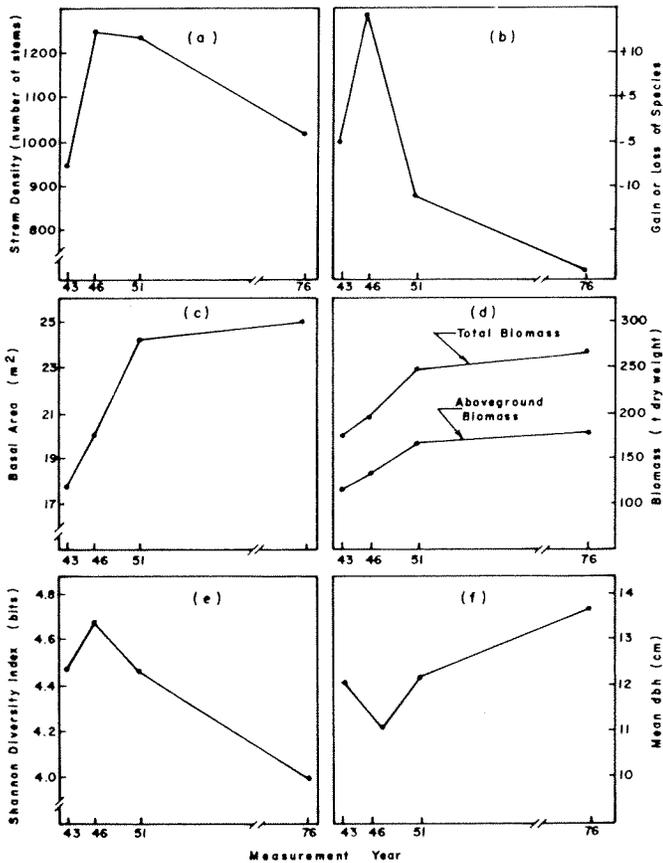


Figure 73.—Changes in stand characteristics for the El Verde plots during the period 1943–1976. Measurements are based on all trees with dbh > 4 cm in 0.75 ha plot (Crow 1980).

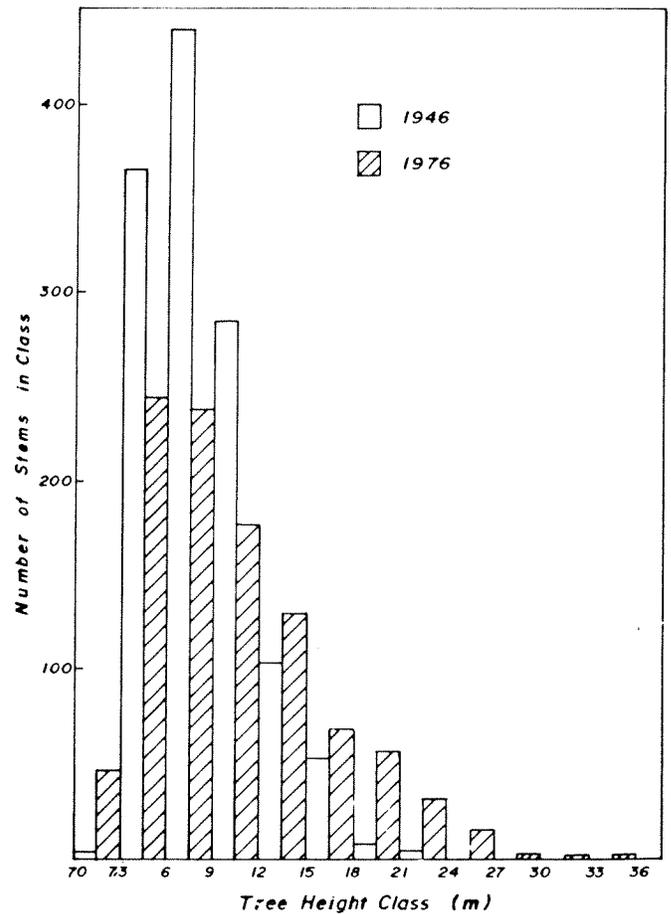


Figure 74.—Distribution of trees by height class in the tabonuco forest at El Verde (Crow 1980).

Table 86.—Mean diameter and basal area increments for species in lightly cut (Sabana 8 and Río Grande) and natural (Sabana 4) stands of tabonuco (Crow and Weaver 1977)

Species	Mean dbh 1975 (cm)	Diameter increment			Mean BA increment (cm ² /yr)	Number observed
		Mean	Range	Coefficient of variation (%)		
Sabana 8						
<i>Alchornea latifolia</i>	24.3	0.38	0.0–1.45	67.9	14.6	199
<i>Buchenavia capitata</i>	35.8	0.68	0.0–1.83	58.9	34.3	30
<i>Byrsonima coriacea</i>	21.7	0.48	0.02–1.02	45.9	14.1	61
<i>Cecropia peltata</i>	31.7	0.51	0.08–1.55	64.5	22.6	49
<i>Dacryodes excelsa</i>	30.1	0.74	0.48–1.32	33.5	28.2	11
<i>Didymopanax morototoni</i>	23.3	0.33	0.0–1.09	71.5	11.1	134
<i>Guarea trichilioides</i>	32.4	0.81	0.13–1.35	46.8	33.2	18
<i>Homalium racemosum</i>	23.3	0.51	0.15–0.91	47.1	15.6	18
<i>Inga laurina</i>	22.8	0.46	0.0–1.17	54.9	15.1	114
<i>Manilkara bidentata</i>	26.3	0.51	0.02–1.12	60.3	22.3	22
<i>Matayba domingensis</i>	24.6	0.56	0.0–1.02	44.0	18.2	24
<i>Nectandra sintenisii</i>	18.3	0.35	0.0–0.65	60.1	9.0	6
<i>Ocotea leucoxyton</i>	19.8	0.35	0.0–1.27	76.6	10.6	115
<i>Ormosia krugii</i>	24.2	0.51	0.0–1.14	44.2	17.2	59
<i>Sloanea berteriana</i>	28.9	0.69	0.15–1.22	54.0	27.7	8
<i>Tabebuia heterophylla</i>	19.0	0.28	0.0–1.04	69.5	8.1	459
<i>Zanthoxylum martinicense</i>	25.1	0.66	0.38–1.14	44.1	21.0	5
Río Grande						
<i>Alchornea latifolia</i>	22.2	0.33	0.02–0.68	69.3	11.7	9
<i>Buchenavia capitata</i>	35.9	0.71	0.08–1.57	74.3	38.4	11
<i>Cecropia peltata</i>	27.0	0.46	0.02–1.09	69.8	16.7	35
<i>Dacryodes excelsa</i>	30.6	0.46	0.0–1.07	54.0	19.1	79
<i>Didymopanax morototoni</i>	23.6	0.31	0.0–0.89	77.1	10.6	36
<i>Homalium racemosum</i>	28.5	0.48	0.10–1.02	50.9	20.1	18
<i>Inga laurina</i>	39.9	0.58	0.18–0.81	42.8	30.7	8
<i>Linociera domingensis</i>	21.2	0.38	0.18–0.63	34.4	12.0	15
<i>Manilkara bidentata</i>	27.8	0.58	0.08–1.14	46.4	23.7	27
<i>Matayba domingensis</i>	21.9	0.38	0.02–1.17	55.1	11.9	63
<i>Ocotea leucoxyton</i>	25.1	0.38	0.05–1.12	74.3	12.9	13
<i>Ormosia krugii</i>	30.5	0.38	0.05–1.32	78.6	17.3	18
<i>Sloanea berteriana</i>	22.3	0.30	0.02–0.86	83.0	10.3	17
<i>Tabebuia heterophylla</i>	22.9	0.35	0.0–0.76	59.7	12.0	55
Sabana 4						
<i>Alchornea latifolia</i>	27.7	0.43	0.02–1.07	73.9	18.7	17
<i>Cecropia peltata</i>	29.1	0.46	0.05–1.24	62.4	17.6	33
<i>Dacryodes excelsa</i>	34.9	0.25	0.0–0.81	63.9	13.4	117
<i>Didymopanax morototoni</i>	31.8	0.53	0.08–1.35	59.3	23.4	23
<i>Inga laurina</i>	26.0	0.43	0.0–0.99	68.1	16.6	28
<i>Linociera domingensis</i>	18.1	0.35	0.13–0.63	59.2	9.4	5
<i>Matayba domingensis</i>	25.8	0.51	0.33–0.74	32.3	16.2	9
<i>Sloanea berteriana</i>	26.9	0.48	0.01–1.35	47.4	19.1	41

Table 87.—Average periodic diameter growth (PAI) and basal area growth for individual trees in the study areas. Means are weighted by number of individuals for each species (Crow and Weaver 1977)

Study area	Sample size	PAI (cm/year)	BA increment (m ² /year)
Sabana 8	1384	0.391	0.188
Río Grande	404	0.419	0.231
Sabana 4	273	0.376	0.234

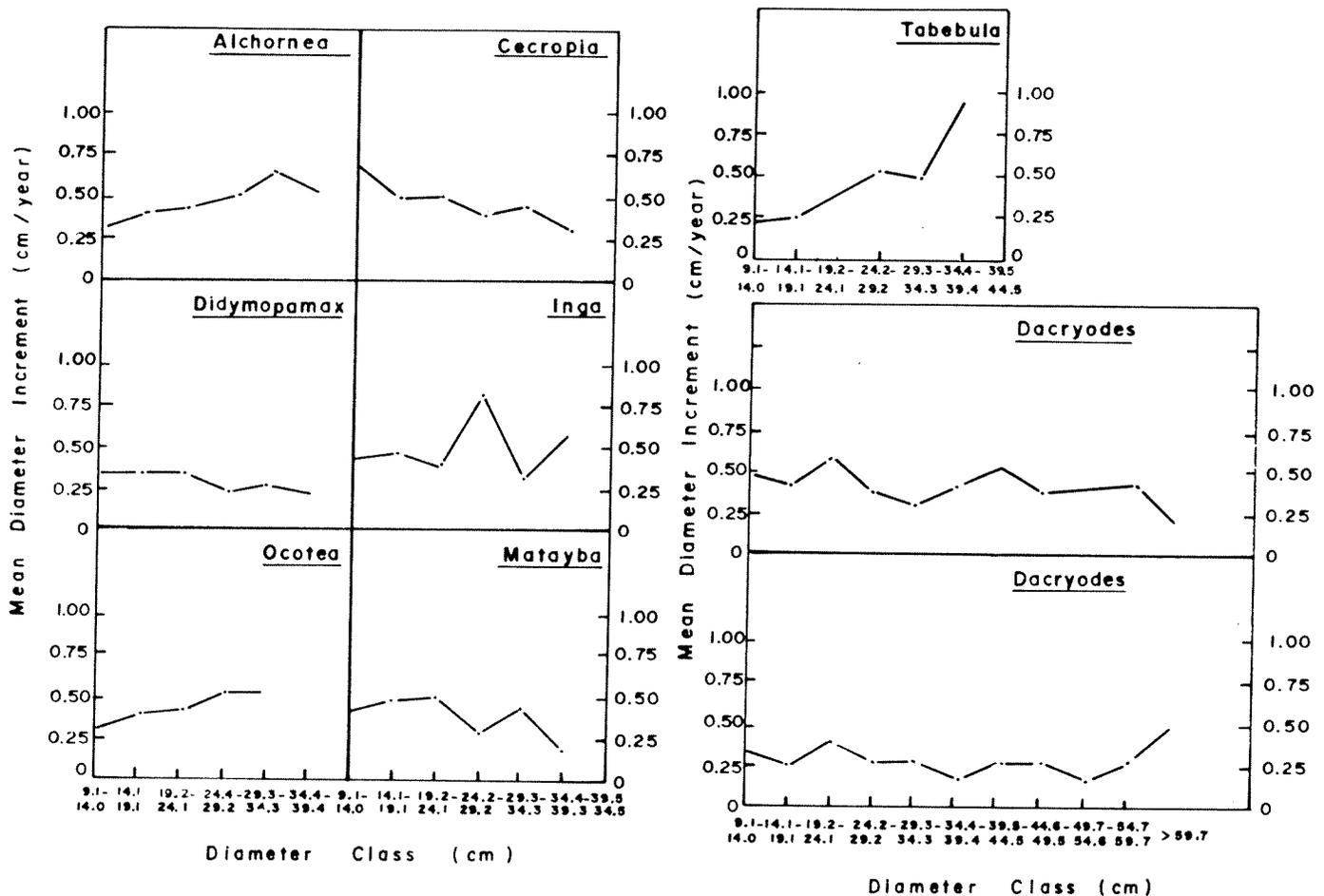


Figure 75.—Relation between mean diameter increment and diameter class at time of measurement (Crow and Weaver 1977).

history stages of one species, *Nasutitermes costalis* (Holmgren) were studied by Weigert (1970b). Workers were by far the most common class, both on the basis of abundance and biomass. In spite of their numerical abundance and conspicuousity, the role of the termite in decomposition is relatively minor as its food supply is restricted to dead wood not yet in an advanced state of decay. The total energy flow of 5 to 6 kcal/m²·yr is only a small fraction of the total input into decomposer-detritus food chains.

Faunal communities contained in bromeliad leaf axils were examined by Maguire (1970) and characterized by association coefficients between various combinations of species groups. In 65 bromeliads examined, 76 types of organisms were identified. In order to characterize communities, 13 associations, 7 positive and 6 negative, were determined to be significant and may indicate similarities and differences in feeding methods and efficiencies.

Herbivory, measured by area of holes in leaves, although conspicuous in some species of trees, varied from 3–8%, less than that in temperate forests (Odum and Ruiz-Reyes 1970).

Amphibians

Amphibians and reptiles, both conspicuous and abundant components of the fauna of the Luquillo Experimental Forest, are only a small fraction (2%) of the animal biomass in the tabonuco forest (c.f. tables 89 and 90). Taxonomic descriptions of the amphibians of Puerto Rico have been given by Gundlach (1887–1894), Stahl (1882), Stehner (1904), Schmidt (1927, 1928), Rivero (1956, 1963, 1978), and Thomas (1965). Rivero (1978) discussed the taxonomy and ecology of all Puerto Rican amphibian and reptile species. Field identification keys and keys to the calls of all frog species have been constructed by Drewry (1970c) and Rivero (1978).

The fauna of the Luquillo Experimental Forest includes 14 of the 22 reported Puerto Rican amphibian species (Drewry 1970c and table 92). Thirteen are endemic frogs belonging to the family Leptodactylidae: *Leptodactylus albilabris* and 12 members of the genus *Eleutherodactylus* (coquies). *Bufo marinus* (family Bufonidae), a toad introduced from Jamaica and Barbados in the 1920's to control the white

Table 88.—Numbers, survival and growth of tree seedlings and seeds planted in the Luquillo Experimental Forest during 1934–1945 (Marrero 1947)

Species	Number seedlings	Weight of seeds (kg)	Survival	Growth
Native				
<i>Andira inermis</i>	1,975		low	slow
<i>Buchenalia capitata</i>	medium
<i>Byrsonima coriacea</i>	19,169		low
<i>Calophyllum calaba</i>	5,755	high	medium
<i>Cedrela odorata</i>	525,950		low
<i>Ceiba pentandra</i>	5,500		low
<i>Cordia alliodora</i>	344,685		medium
<i>Dacryodes excelsa</i>		low	medium
<i>Eugenia stahlia</i>		high	slow
<i>Guarea guidonia</i>	63,891		high	medium-slow
<i>Hymenea courbaril</i>	3,900	277	low	slow
<i>Manilkara bidentata</i>	19,450		high	fast
<i>Montezuma speciosissima</i>	206,359		high	fast
<i>Ocotea moschata</i>	227	medium
<i>Petitia domingensis</i>	191,105		high	medium
<i>Pouteria multiflora</i>		medium-high	fast
<i>Sideroxylon foetidissimum</i>	2,902	low
<i>Tabebuia heterophylla</i>	232,625		high	slow
<i>Vitex divaricata</i>	9,300		medium	slow
Total	1,623,909			
Exotic				
<i>Albizia lebbbeck</i>	46,150		medium
<i>Bambusa spp.</i>
<i>Casuarina equisetifolia</i>	121,770		low
<i>Dalbergia sissoo</i>	60,920		low	slow
<i>Eucalyptus spp.</i>	24,440		high	medium
<i>Eugenia jambos</i>	1,975		medium	medium
<i>Cassia siamea</i>	43,155		medium
<i>Swietenia macrophylla</i>	1,106,202		high	medium
<i>Swietenia mahagoni</i>	963,902		low-medium	slow
<i>Tectona grandis</i>	63,543		low	slow
Total	2,432,057			

grub of sugar cane (Rivero 1978), has become common in Puerto Rico. This toad is abundant in the Luquillo Experimental Forest in areas with bare earth and pavement. However, it returns to still bodies of water at lower elevations for breeding.

Distribution, reproductive behavior, vocalization, territoriality, habitat and karyotypes of the 12 species of "coquies" (*Eleutherodactylus* and *L. albilabris*) were reviewed and investigated by Drewry (1970b, 1970c). Species composition differs with elevation and for each species a distinct habitat may be described. *Leptodactylus albilabris*, *E. coqui*, *E. brittoni* and *E. antillensis* are found throughout the island at most elevations. *Leptodactylus albilabris* is primarily terrestrial and particularly abundant in or near streams, ditches, and marshy areas where the forest is not dense. In contrast to *E. spp.*, in which development is direct, *L. albilabris* is one of the two native Puerto Rican amphibian species which passes

through a tadpole stage. Eggs hatch into aquatic larvae under conditions of abundant food and water but with increasing water stress, direct development (no tadpole stage) occurs.

Although found throughout the island, the abundance of *E. brittoni* and *E. antillensis* diminishes with increasing altitude in the Luquillo Mountains. At lower elevations these species are most commonly found on low vegetation in sunny areas such as meadows and road cuts. The latter species appears to prefer broad-leaved plants, while the former prefers grasses. A commonly used index of arboreality is the ratio of toe pad diameter to body weight. *Eleutherodactylus coqui*, with a high ratio, is an arboreal species which frequents shaded areas on wall surfaces and leaf axils at any height above ground.

Restricted to the island's montane forest are *E. Karlschmidti*, *E. unicolor*, *E. hedriki*, *E. eneidae*, *E. locustus*, *E. gryllus*, *E. portoricensis*, *E. wightmanae*,

Table 89.—Bases for estimation of biomass of herbivores and carnivores (Odum et al. 1970a)

(All weights dry; ind. = individual)

Trophic level and component	Basis for estimate with original counts in parentheses	Biomass (g/m ²)		
		Jan. 1958	May 1959	Mean
HERBIVORE DECOMPOSERS				
Social insect colonies on the ground	956 (100, 225, 500, 3000) insects/colony; 2.2 mg/ind.; 1.7 (1, 2, 2) colonies/25-m ² area	0.143		
	43/25 m ² (3, 1, 125); 956 ind./colony; 9 mg/ind.		1.48	0.81*
Larger leaf-litter animals		0.13		
Ants	11 (1, 1, 30)/25-m ² quadrat; 0.3 g/ind.			
Millipedes	11 (31, 4, 0)/25 m ² ; 9 mg/ind.			
Roaches	9.3 (0, 25, 3)/25 m ² ; 26.4 mg/ind.			
Worms	18 (10, 29, 15)/25 m ² ; 2.5 mg/ind.			
Snails	0.7 (1, 1, 0)/25 m ² ; 53.6 mg/ind.			
Slugs	6.7 (4, 1, 0)/25 m ² ; 2 mg/ind.			
Isopods	0.7 (2, 0, 0)/25 m ² ; 30 mg/ind.			
Centipedes	1.7 (5, 0, 0)/25 m ² ; 2 mg/ind.			
	2.6 (8, 0, 0)/25 m ² ; 20 mg/ind.			
			Totals 0.029	0.079*
Soil fauna			0.28*	
Worms	5/m ² ; 53.6 mg/ind.			
Mites	150/m ² ; 0.1 mg/ind.			
Soil microzoa from extractor (see Chap. H-4)	Total arthropods in 3 layers: litter, 23,160/m ² ; top soil, 22,540/m ² ; 5-cm depth, 4210/m ² ; est. dry weight of each, 0.017 mg. (85 ants weighed 1.42 mg)	0.85*		
Insects in crown leaves of Tabonuco				
Orthoptera	0.030 (0.007; 0.047; 0.031; 0.012; 0.028; 0.047)/leaf; 2 mg/ind.; 100 to 500 leaves/sample; 700 leaves/m ²			
Ants	0.048 (0.074; 0.074; 0.028; 0.028; 0.024; 0.062)/leaf; 9 mg/ind.			
Large insects	0.008 (0.001; 0.005; 0.012; 0.012)/leaf; 137 mg/ind.		Total 0.84	
	1.9 ind./100 leaves (3/142; 5/303); 1 mg/ind.; 700 leaves/m ²	0.0013		0.43*
Insects in crown of ferns and palms	30 (60, 0)/tree; 11 trees/900 m ² ; 1 mg/ind.	0.0004*		
Small insects on smaller branches (1 in. to petiole)	23 (24, 21) ind./linear m of branch; 1 mg/ind.; 107 m of branches/tree; 69 trees/900 m ²	0.19*		
Insects on lianas	250 ind./linear m; 12 m/liana; 0.127 liana/m ² ; 0.5 mg/ind.	0.19*		
Small insects on larger branches and trunks	53 (80, 70, 9)/linear m of branch; 105 m of branch/tree; 69 larger trees/900 m ² ; 1 mg/ind.	0.42		
	257 (177, 700, 0, 153)/m ² ; 1 mg/ind.; 7 m ² of trunk area/tree; 0.077 large trees/m ²	0.14		
Ants	3.3 (3, 5, 2)/0.69 m ² ; 0.9 mg/ind.		0.0043	
Small insects	5.3 (7, 1, 8)/0.69 m ² ; 1 mg/ind.		0.0077	
Large insects	3/0.69 m ² ; 137 mg/ind.		0.60	
			0.90	
		Total 0.56	0.61	0.58*
Flying day insects	1.5 (3, 0, 1, 1, 1, 3) counted per 400 m ² /hr; 0.3 g dry ind.	0.0011*		
Flying night insects	1.4 (0.1; 1; 2; 1; 3; 2) counted/100 sec (10 flash views of 10 sec duration); 20 m ² of forest viewed; forest depth, 15 m; 0.3 mg/ind.	0.002*		

(All weights dry; ind. = individual)

Trophic level and component	Basis for estimate with original counts in parentheses	Biomass (g/m ²)		
		Jan. 1958	May 1959	Mean
HERBIVORE DECOMPOSERS				
Birds other than bananaquits	See table 5	0.0008*		
Bananaquits	See calculation in section of this table on Carnivores. Food is 50% vegetable (table 5).	0.0035*		
Snails				
Large snails	1.3 (0, 3, 1)/25-m ² quadrat; 0.94 dry g (not shell)/ind.	0.049		
Small snails	8 (9, 7, 7) ind./25 m ² ; 0.03 dry g tissue/ind.	0.01		
In trees	4 (3, 3, 6)/25 m ² ; 24 mg/ind.		0.0038	
On ground	10 (3, 17)/25 m ² ; 34 mg/ind.		0.0136	
	Total	0.059	0.0174	0.038*
Rats	0.003/m ² (17 ind./5200 m ² of trap area (see table 6); 170 g wet/ind.; 25% dry of wet	0.12*		
Insects in bromeliads	54/bromeliad; 2.5 mg/ind.; 27 bromeliads/ 900 m ²	0.004*		
	Total dry weight of herbivore decomposers (sum of figures with "**")	3.579		
CARNIVORES				
Lizards	3 (4, 1, 4)/25 m ² 2.5 (3, 4)/25 m ² ; 5.5 (5, 6)/6/ 25 m ² ; 0.57 g/ind. [Sic]	0.057	0.103	0.080*
Frogs				
Ground	1.7 (1, 3, 1) ind./25 m ² ; 0.55 g/ind.	0.037		
Lower story	1 (2, 0)/25 m ² ; 0.16 g/ind.		0.0062	0.02*
Voice census of <i>Eleutherodactylus portoricensis</i> in trees	0.0013 (0.001; 0.001; 0.001; 0.002) ind./m ² ; 1.8 g/ind.		0.0023*	
Bananaquits	70 ind./27,400 m ² (table 5); 3 g/ind.; 50% of food of animal origin	0.0035*		
Other birds	See table 5; 4.2 g/ind.	0.0016*		
Bats	0.6% of one ind./400 m ² based on a time count (0.06/min; 0.4/min; 0.11/min); each bat present ~5 sec when observed; 10g/ind.	0.00015*		
Spiders	5 larger ind./10,900 leaves; 0.025 g/ind.; 700 leaves/m ²	0.0081*		
	9 (13, 5) medium ind./sapling/m ² ; 0.4 sapling/m ² , 0.01 g/ind.	0.036*		
	22 smallest ind./m ³ of forest volume on night counts; 15-m height; 0.001 g/ind.	0.33*		
	135/25 m ² (ground count: 47, 33, 325); 0.025 g/ind.		0.135*	
	0.01 ind./leaf count (0.003; 0.008; 0.012; 0.012; 0.025; 0.006; 0.005); 0.002 g/ind.;		0.014	
	100/to 500 leaves/count; 700 leaves/m ²		0.0008	
	8 webs/25 m ²			
	Total	0.46	0.15	0.30
Total dry weight of carnivores (sum of data marked with *)				0.62
Total dry weight of animals (sum of herbivores and carnivores)				4.20
Weight projected trigonometrically from 50* to the horizontal plane				6.60

and *E. richmondi*. The distribution of *E. karlschmidti* is unique, being found only near fast moving streams. It has a high ratio of toe pad diameter to body weight and extremely large eyes relative to body size. This frog inhabits crevices and surfaces of boulders. Rivero et al. (1963) found that a high proportion of its food (32.4%) was aquatic. *Eleutherodactylus unicolor* is restricted to saturated soil of the high elevation dwarf forest. As a result of this limited natural habitat, the species has been classified as threatened by the Department of Natural Resources of the Commonwealth of Puerto Rico (Raffaele 1977). *Eleutherodactylus hedriki* is found at low elevations and is restricted to deep forest shade. This species is arboreal and most frequently found in tree holes at any height above ground.

Abundance of the remaining species generally increases with altitude. The range of *E. eneidae*, *E. locustus* and *E. gryllus* does not extend below 275 m. *Eleutherodactylus eneidae*, found within the forest and towards the forest edge, frequents the moss on stones, tree trunks and earth banks. *Eleutherodactylus locustus* and *E. gryllus* are, however, restricted to the forest edge in dense but well lighted thickets and fern banks. *Eleutherodactylus gryllus* appears to prefer bromeliads and broad leaved vegetation.

The range of *E. portoricensis*, *E. wightmanae* and *E. richmondi* extends as low as 100 m. The latter two species are found towards the forest edge and both, with low toe pad diameter to body weight ratios, are primarily terrestrial. *Eleutherodactylus wightmanae* is abundant in litter and decaying wood. *Eleutherodactylus portoricensis* is restricted to the deep forest, commonly found in leaf axils and under bark at heights of up to 4 m above the ground.

Descriptive studies indicated that the order of overall abundance of the five more common species in the tabonuco forest at El Verde was *E. wight-*

Table 90.—Animal biomass in the El Verde forest (Odum 1970b)

Material	Dry weight, g/m ²
Animal biomass estimated in Sabana plots	6.8*
Corrections and additions	
Termites	0.6*
Earthworms	4.2*
Nematodes	0.0090*
Coquis	0.18†
Caracolas	0.12
Birds	0.008
Overall estimate for Tabonuco forest type, sum of values with*.	11.8

†(1.8 g each) (0.1 individuals/m²).

manae, *E. portoricensis*, *E. richmondi*, *E. eneidae* and *E. hedriki* (Turner and Gist 1970). Population estimates of the more vocal species, *E. portoricensis*, suggested a density of 162 males/ha.

The coexistence of numerous species of frogs of the same genus has stimulated investigation of their ecology in order to further define the niches occupied by each. The stomachs of ground dwellers (*E. wightmanae*, *E. portoricensis*, *E. eneidae*, *E. richmondi*, and *E. locustus*) contained a high percent of prey from the litter complex (fig. 77). Cintrón (1970a) found that three species of frogs in the tabonuco forest were associated with different parts of the vegetation (fig. 78). However, stomach analyses indicated that similar species and sizes of food had been consumed.

Species also differ in types and timing of nocturnal calling activity (Drewry 1970c; Rivero 1978). All species but *E. eneidae* begin calling at sunset (fig. 79). Avoiding acoustical competition, *E. eneidae* calls

Table 91.—Number of individuals and of species collected in the three centers of the El Verde site (McMahan and Sollins 1970)

Center	No. of individuals (including larvae and nymphs)	Omitting larvae and nymphs			
		No. of individuals	No. of species	Diversity index	
				Species/ $\sqrt{\text{ind.}}$	Species/1000 ind.
South Control	1355	1252	122	3.45	97
Radiation	2072	1162	139	4.08	120
North Cut	1604	1458	149	3.90	102
Total	5031	3872	313*	5.03	81

*Total number of species does not equal the sum of the species for the three centers because of species overlap in the three.

Table 92.—*Terrestrial fauna of the Luquillo Experimental Forest*

Classification	Spanish name
MAMMALIA	
Order Chiroptera (Bats)	
Family Mormoopidae	
<i>Pteronotus fuliginosus</i>	murcielago bigotudo
<i>Mormoops blainwillii</i>	murcielago canela
Family Phyllostomatidae	
<i>Monophyllus redmani</i>	murcielago de lengua larga
<i>Artibeus jamaicensis</i>	murcielago frutero
<i>Stenoderma rufum</i>	murcielago rojo
<i>Brachyphylla cavernarum</i>	murcielago cavernicola
<i>Erophylla bombifrons</i>	murcielago de flores
Family Vespertilionidae	
<i>Eptesicus fuscus</i>	murcielago pardo
<i>Lasiurus borealis</i>	murcielago rojo
Family Molossidae	
<i>Tadarida brasiliensis</i>	murcielago rabilargo
<i>Molossus molossus fortis</i>	murcielago casero
Order Rodentia	
Family Muridae	
<i>Rattus rattus</i>	rata negra
<i>Rattus norvegicus</i>	rata de noruega
Order Carnivora	
Family Viverridae	
<i>Herpestes javanicus auropunctatus</i>	mangosta de la india
Family Felidae	
<i>Felix catus</i>	gato feral de mona
REPTILIA	
Order Serpentes	
Family Typhlopidae	
<i>Typhlops</i> sp.	
Family Boidae	
<i>Epicrates inornatus</i>	culebrón
Family Colubridae	
<i>Alsophis portoricensis</i>	culebra
Order Sauria	
Family Iguanidae	
<i>Anolis gundlachi</i>	lagartijo de ojos azules
<i>A. evermanni</i>	lagartijo verde
<i>A. stratulus</i>	lagartijo manchado
<i>A. cuvieri</i>	lagarto verde
<i>A. cristatellus</i>	lagartijo comun
<i>A. krugi</i>	lagartijo con mancha detrás de ojos
<i>A. occultus</i>	
<i>A. pulchellus</i>	
Family Gekkonidae	
<i>Sphaerodactylus macrolepis</i>	
Family Anguidae	
<i>Diphloglossus pleei</i>	culebra de cuatro patas
AMPHIBIA	
Order Salientia	
Family Leptodactylidae	
<i>Eleutherodactylus portoricensis</i>	coquí montano
<i>E. wightmanae</i>	coquí melodioso
<i>E. richmondi</i>	coquí de richmond
<i>E. hedricki</i>	coquí de hendricks
<i>E. coqui</i>	coquí común
<i>E. antillensis</i>	coquí de campo
<i>E. brittoni</i>	coquí de graminas
<i>E. locustus</i>	rana locusta
<i>E. gryllus</i>	coquí grillo

Table 92.—*Terrestrial fauna of the Luquillo Experimental Forest—Continued*

Classification	Spanish name
<i>E. karlschmidti</i>	coquí palmeado
<i>E. unicolor</i>	ranita duende
<i>E. eneidae</i>	coquí de eneida
<i>Leptodactylus albilabris</i>	sapito de pantanos
Family Bufonidae	
<i>Bufo marinus</i>	sapo concho común
AVES	
Family Accipitridae	
<i>Accipiter striatus</i>	halcón de sierra
<i>Buteo jamaicensis</i>	guaragua
<i>B. platypterus</i>	guaraguaito
Family Columbidae	
<i>Columba squamosa</i>	paloma turca
<i>Zenaida aurita</i>	tortola
<i>Geotrygon montana</i>	perdiz
Family Psittacidae	
<i>Amazona vittata vittata</i>	cotorra
Family Cuculidae	
<i>Saurothera vieilloti</i>	pajaro
<i>Crotophaga ani</i>	judío
Family Strigidae	
<i>Otus nudipes</i>	múcaro
Family Apodidae	
<i>Cypsiloides niger</i>	vencejo
Family Trochilidae	
<i>Chlorostilbon maugaeus</i>	zumbadorcito
<i>Anthracothorax viridis</i>	zumbador verde
Family Todidae	
<i>Todus mexicanus</i>	san pedrito
Family Picidae	
<i>Melanerpes portoricensis</i>	carpintero
Family Tyrannidae	
<i>Tyrannus dominicensis</i>	pitirre
<i>T. caudifasciatus</i>	clérigo
Family Hirundinidae	
<i>Hirundo rustica</i>	golondrina de horguilla
<i>Petrochelidon fulva</i>	golondrina de cuevas
Family Mimidae	
<i>Mimus polyglottos</i>	ruiseñor
<i>Margarops fuscatus</i>	zorzal pardo
Family Turdidae	
<i>Mimicichla plumbea</i>	zorzal azul
Family Vireonidae	
<i>Vireo altiloquus</i>	julián chiví
<i>V. latimeri</i>	bien-te-veo
Family Parulidae	
<i>Mniotilta varia</i>	reinita trepadora
<i>Parula americana</i>	reinita pechidorada
<i>Dendroica tigrina</i>	reinita dencosta
<i>D. caerulescens</i>	reinita azul
<i>Seiurus motacilla</i>	pizpito de río
<i>Setophaga ruticilla</i>	candelita
Family Thraupidae	
<i>Tanagra musica</i>	canario del país
<i>Spindalis zena</i>	reina mora
<i>Nesospingus speculiferus</i>	llorosa
Family Fringillidae	
<i>Tiaris olivacea</i>	gorrión barba amarilla
<i>T. bicolor</i>	gorrión negro
<i>Loxigilla portoricensis</i>	come ñame

Table 92.—*Terrestrial fauna of the Luquillo Experimental Forest—Continued*

Classification	Spanish name
Family Coerebidae	
<i>Coereba flaveola</i>	reinita común
Family Ploceidae	
<i>Lonchura cucullata</i>	diablito
Family Icteridae	
<i>Icterus dominicensis</i>	calandria
<i>Guiscaulus niger</i>	mozambique
<i>Molothrus bonariensis</i>	tordo
FAUNA (Aquatic)	
Phylum Chordata	
Class Osteichthyes	
Family Gobiidae	
<i>Scicydium plumieri</i>	chupa piedra
Phylum Arthropoda	
Class Crustacea	
Order Decapoda	
Family Atyidae	
<i>Atya scabra</i>	
<i>A. lanipes</i>	chájara
<i>A. innocous</i>	
<i>Xiphocaris elongata</i>	salpiche
Family Potamonidae	
<i>Epilobocera situatifrons</i>	buraquena
Family Palaemonidae	
<i>Macrobrachium carcinus</i>	
<i>M. heterochirus</i>	
<i>M. crenulatum</i>	
<i>M. acanthurus</i>	
Drifting invertebrate larvae	
Order Diptera	
Order Trichoptera	
Order Ephemeroptera	
Order Hydracarina	
Order Odonata	
Phylum Mollusca	
Family Neritidae	
<i>Neritina reclinata</i>	
Family Thiaridae	
<i>Tarebia granifera</i>	
Family Pilidae	
<i>Marisa cornuarietis</i>	

only sporadically before 10 pm, and peak activity occurs at 2 am. Investigation by Drewry (1970c) and others have emphasized the importance of calling in maintenance of intraspecific and perhaps interspecific territoriality. Species of *Eleutherodactylus* maintain three types of territories. The first, primarily for shelter, is defended by all adults, but the second, a feeding territory, is defended only by females. The most conspicuous calls are emitted by males in defense of the mating territory. Each species has a characteristic call (Drewry 1970c). *Eleutherodactylus coqui* and *E. portoricensis*, recognized as separate species only relatively recently, are distinguished by the rate of calling in each call group (Thomas 1965). *Eleutherodactylus coqui* is found throughout the is-

land in both the highlands and lowlands, but *E. portoricensis* is restricted to the mountains. Where their ranges overlap *E. portoricensis* is found more often at ground level and its food includes a greater proportion of terrestrial insect species (Rivero 1978).

Reptiles

The fourteen species of reptiles known to inhabit the Luquillo Experimental Forest (listed in table 92) have been taxonomically described by Gundlach (1887–1894), Stehneger (1904), Schmidt (1927, 1928), Schwartz (1967), Thomas (1966), and Rivero (1978).

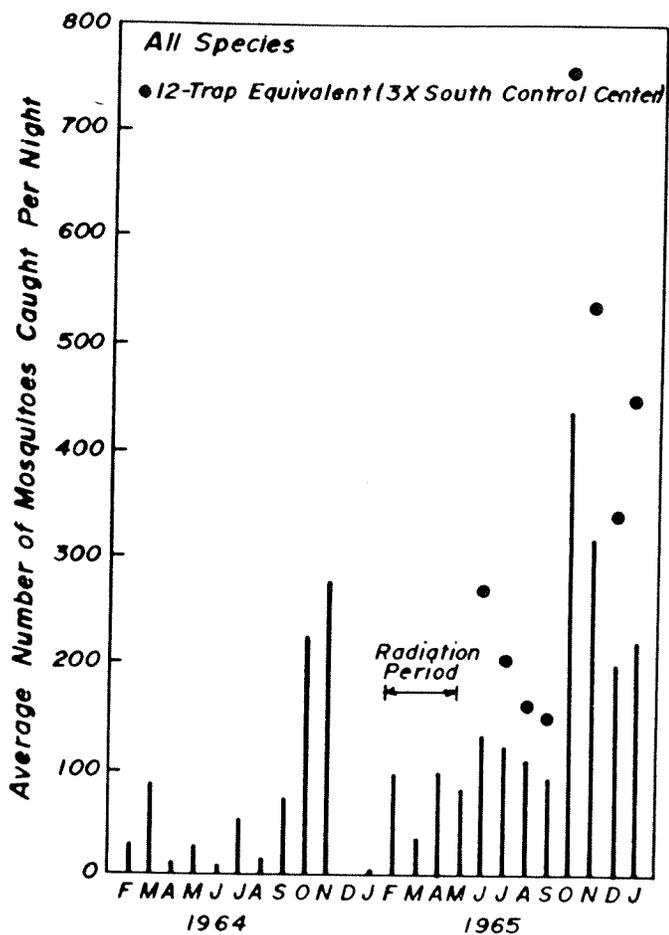


Figure 76.—Monthly record of mosquitoes caught in the tabonuco forest at El Verde (Weinbren and Weinbren 1970).

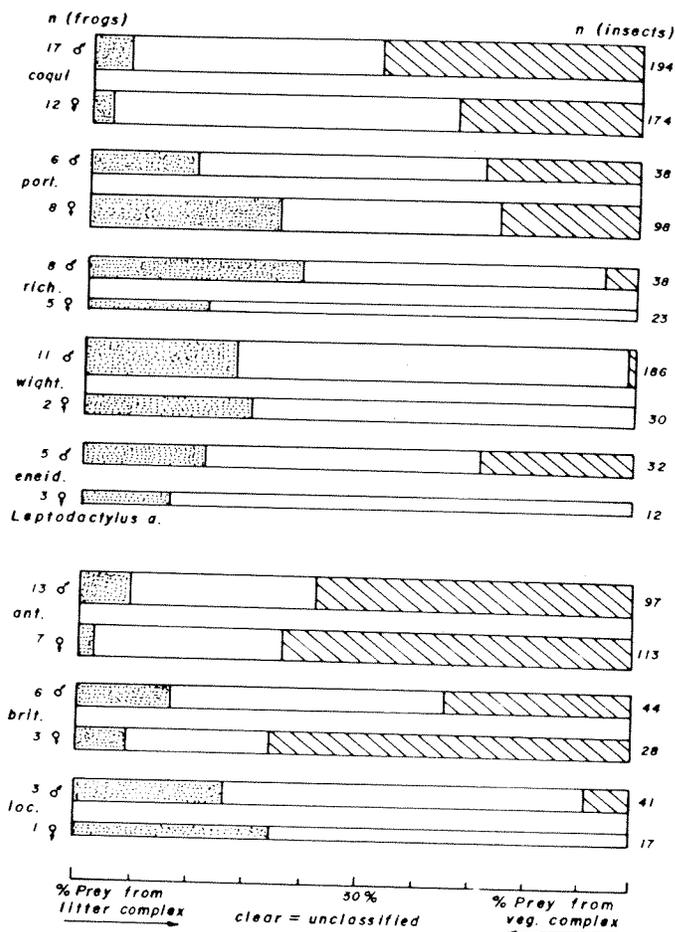


Figure 77.—Feeding behavior of *Leptodactylus albilabris* and species of *Eleutherodactylus* (Lavigne and Drewry 1970).

Eight of these reptiles are lizards of the genus *Anolis*, the most common group of diurnal vertebrates in the West Indies. As with amphibians, numerous species belonging to the same genus inhabit the same areas. Rand (1964) defined two sets of ecological factors involved in their habitat segregation. The first, "structural habitat", refers to the different size and position of perches utilized by each species during their daytime search for food. The second, "climatic habitat," refers to the preference for sun or shade. Highland species, preferring shady situations, were shown to have a lower body temperature than those lowland species preferring sunnier areas (Rand 1964).

On the basis of "structural habitat" or perch height and diameter, three groups may be distinguished. *Anolis krugi* and *A. pulchellus* are found on small perches below 1 m, *A. evermanni* and *A. stratulus* on large diameter perches from 1 to 3 m above ground, and *A. gundlachi* and *A. cristatellus* on moderate to large diameter perches close to the ground. Pairs of species with the same "structural habitat" tend to be similar morphologically.

Species within each group occupy different "climatic habitats" (table 93). *Anolis krugi*, *A. evermanni* and *A. gundlachi* may be considered highland and *A. stratulus*, *A. cristatellus* and *A. pulchellus* lowland. When found together at intermediate elevations, highland species show a preference for shaded areas and lowland species for sunnier perches. Only at extreme elevations, e.g. La Mina (800 m) and the coastal plains, do the two groups occur separately. Rand (1964) suggests that this type of structural and climatic separation reduces interspecific competition.

More recently, Moll (1978) investigated *Anolis* lizard's relative abundance in the Luquillo Experimental Forest and its relationship to the change of several climatic factors, food abundance, and available surface area with altitude. In addition, Moll (1978) quantified perch height, diameter and climatic preferences. Coincident with the change in species composition with increasing altitude is a decrease in total abundance of *Anolis*, its prey, abundance of insects, and available surface area.

Anolis cuvieri and *A. occultus* have been excluded

Table 93.—Abundance of the *Anolis* species (shown in percent of total number of observations) found in four forest habitats, number 1–4, in order of increasing elevation. Numbers in parenthesis are the total observations for each species at the given site (Moll 1978)

Species	Anolis climatic habitat in %											
	Stations											
	1			2			3			4		
	sun	s/sd	shade	sun	s/sd	shade	sun	s/sd	shade	sun	s/sd	shade
<i>gundlachi</i>	7.2	10.4	82.4	9.8	9.8	80.4	3.4	21.6	75.0			
	(125)			(92)			(88)					
<i>evermanni</i>	83.3	16.7		24.7	18.5	56.8	6.7	53.3	40.0			
	(6)			(81)			(15)					
<i>stratulus</i>				16.7	50.0	33.3	38.5	15.4	46.2	61.1	5.6	33.3
				(6)			(13)			(36)		
<i>cuvieri</i>												100.0
				(1)								
<i>crisatellus</i>							33.3		66.7	74.0	4.0	22.0
							(3)			(50)		
<i>krugi</i>							25.0	37.5	37.5			
							(8)					
<i>pulchellus</i>										84.6	15.4	
										(13)		

from the majority of studies because of their inaccessible habitats. *Anolis cuvieri*, the largest anole, is restricted to tree crowns in forested areas. *Anolis occultus*, the dwarf anole, is also restricted to tree crowns at elevations greater than 500 m. Both species are considered to be the most primitive anoles in Puerto Rico (Rivero 1978).

The most abundant reptile in the closed tabonuco forest was *A. gundlachi* (Turner and Gist 1970). Population studies of *A. gundlachi* suggested a density of 324/ha, considerably greater than that of comparable species in temperate forests. *Anolis evermanni*, more frequently observed during rainy periods, occupied higher and thicker perches. The greater distance between recaptures indicated that this species may be more agile than *A. gundlachi*. Population studies also included growth rates and (fig. 80) size class distribution (fig. 81).

Seasonality of ovarian (Gorman and Licht 1974) and testis cycles (Licht and Gorman 1975) of anoles have been shown to be more significant in highland species and highland populations of lowland species. Egg production, testis weight, and spermatogenic and androgenic activity peak between March and August and decrease in the fall and winter months (fig. 82 and 83). This decrease was greater, often resulting in a complete cessation, and occurred earlier at higher elevations. Translocation studies with *A. krugi*, *A. stratulus*, and *A. crisatellus* showed that this altitudinal cline in activity is climatically and not genetically induced. Elsewhere such phenological pat-

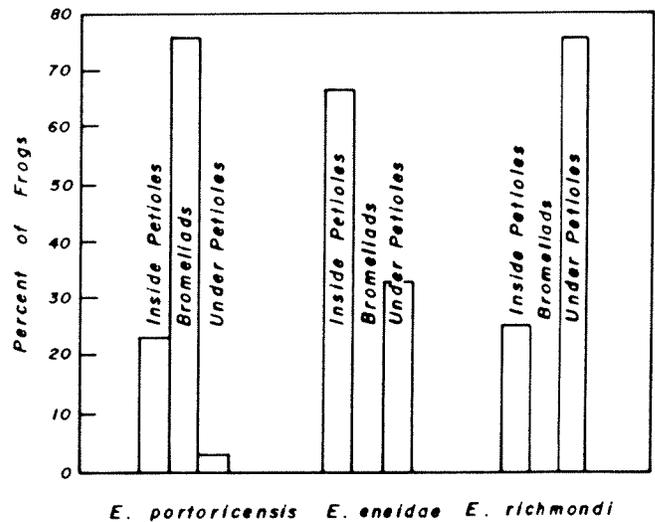


Figure 78.—Distribution of three species of tree frogs (*Eleutherodactylus*) collected in the tabonuco forest at El Verde (Cintrón 1970a).

terns have been attributed to differences in precipitation, however, Licht and Gorman (1975) cite temperature and daylength as causative factors. Low winter temperatures may prolong development and decrease hatchability of eggs.

Three species of nonpoisonous snakes, all endemic, have been reported from the Luquillo Experimental Forest. Turner and Gist (1970) collected a subter-

ranean species, *Typhlops*, from El Verde. *Epicrates inornatus*, the Puerto Rican boa, is the only boa found on the island and has been placed on the federal Endangered Species List. Although the practice is now illegal, in the past the boa was captured in large numbers for extraction of its oil. This and heavy predation by introduced rats and mongooses have placed the boa and *Alsophis portoricensis*, a third species of snake, on the Department of Natural Resources (DNR) list of species in danger of extinction (Raffaele 1977).

The snake-lizards, two secretive species, have been reported in the forest, but little is known of their life histories. *Amphisbaena caeca*, a limbless lizard, constructs burrows in the ground. *Diphloglossus pleei*, and elongate lizard with short, weak limbs, burrows under logs and in leaf litter. The latter species has also been classified by DNR as in danger of extinction (Raffaele 1977). In the Luquillo Experimental Forest and also widespread in Puerto Rico is *Spaerodactylus macrolepis*, (Santa Lucia), the gecko or salamandrita which inhabits the litter layer and lower surface of logs and stones (Schmidt 1928).

Birds

The 108 species of resident birds, as well as migrants, have been described by Wetmore (1916, 1925), Danforth (1931), Bond (1961) and Rolle

(1961). Density of birds in the Luquillo Mountains is similar to that of other tropical rain forests; however, species diversity is lower (Recher and Recher 1966). Recher and Recher (1966) report 39 species from the Luquillo Mountains and more recently Kepler and Parkes (1972) have added a new species, *Dendroica angelae* (dwarf forest warbler) found only in the dwarf forest of the Luquillo Experimental Forest and Maricao (table 92). This low species diversity has been attributed to the depauperate island fauna as a food source and the convergence of the food web (Recher 1970). MacArthur et al. (1966) made comparisons of species diversity in the Luquillo Experimental Forest with that of other temperate and tropical regions. They concluded that, although Puerto Rico had as many species per vegetation layer as Panama and temperate regions, these species do not recognize as many vegetation layers and they sub-divide habitats less. Therefore, completely different habitats may have similar species composition.

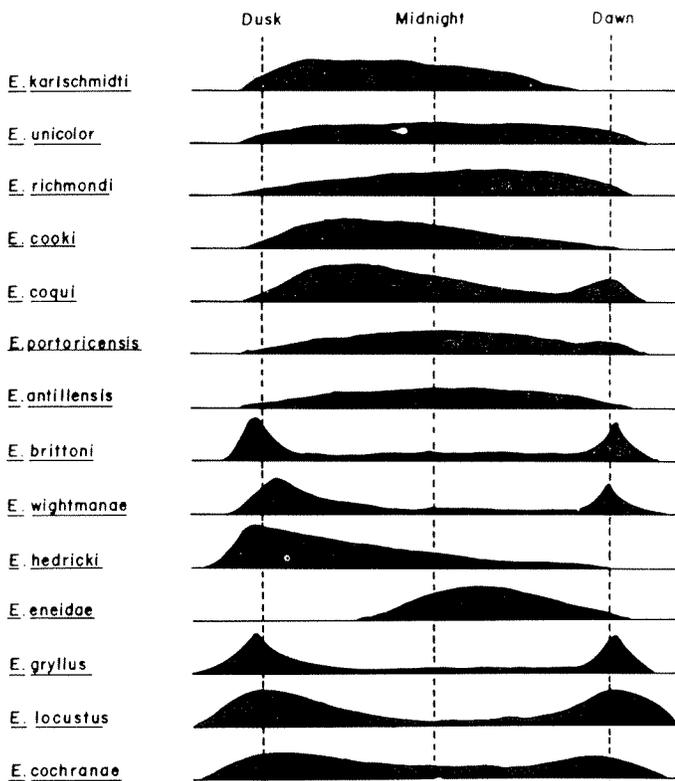


Figure 79.—Vocal activity patterns of Puerto Rican Eleutherodactylus (Drewry 1970c).

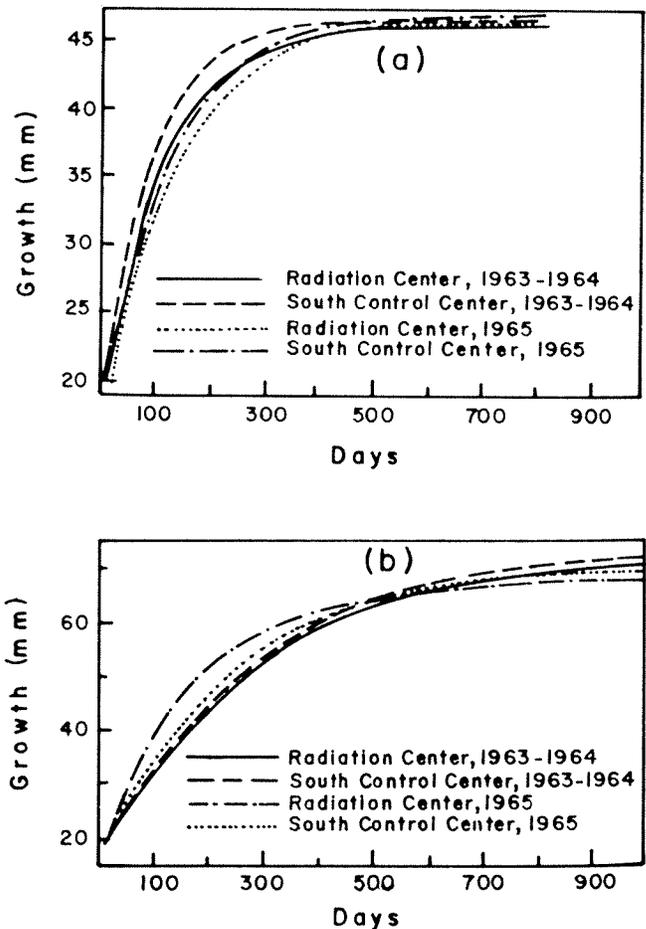


Figure 80.—Growth of (a) male and (b) female *Anolis gundlachi* in the tabonuco forest at El Verde (Turner and Gist 1970).

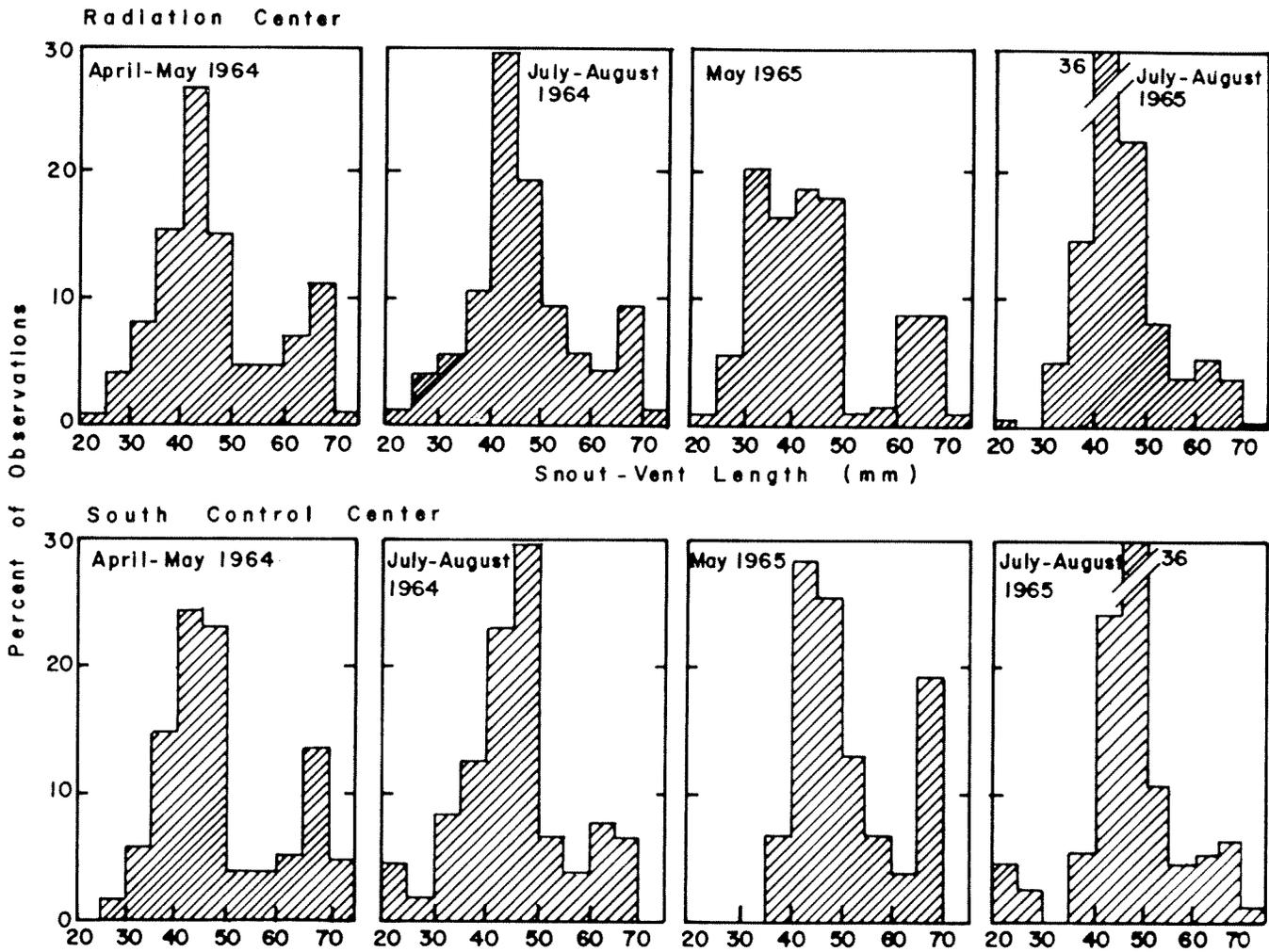


Figure 81.—Size distribution of *Anolis gundlachi* in the tabonuco forest study sites at El Verde (Turner and Gist 1970).

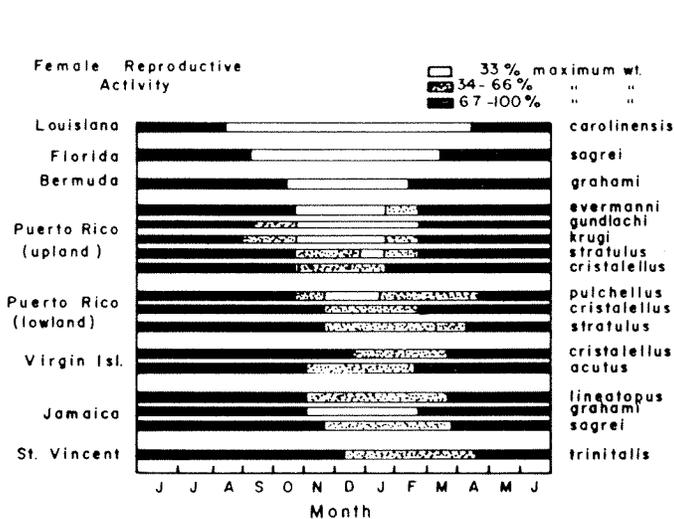


Figure 82.—Seasonality in ovarian activity of lowland and upland populations of species of *Anolis* (Gorman and Licht 1974).

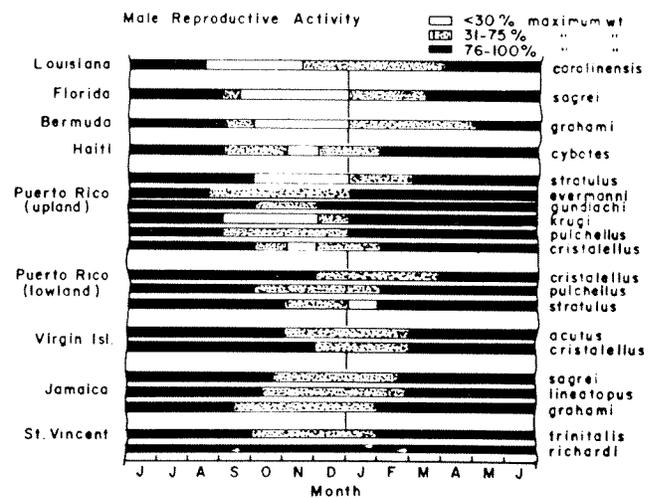


Figure 83.—Seasonality in testicular activity of lowland and upland populations of species of *Anolis* (Licht and Gorman 1975).

Seasonal changes of the avifauna in the tabonuco forest (El Verde, 450 m) were compared to those in the palm forest (Mt. Britton, 850 m) (tables 94 and 95). Species composition was similar in both areas and the banaquit (*Coereba flaveola*) was the most abundant species in each, comprising 55% of the avifauna at El Verde and 64% at Mt. Britton. Bird density, however, was higher in El Verde than in Mt. Britton during every season. This superabundance of a single species, unusual in tropical regions, has been attributed to the absence of effective competitors feeding in a similar manner (Recher 1970). The life history of this bird has been studied by Biaggi (1955). Recher (1970) noted that species composition of the avifauna changed from season to season and year to year as a result of the formation of aggregations and foraging flocks by some species and the arrival of transient and wintering species.

Peak breeding occurs from March to May with the onset of rains. Only the dominant banaquit breeds throughout the year (fig. 84). During the breeding season, Recher (1970) observed defense of territories by the black whiskered vireo, pearly-eyed thrasher, emerald hummingbird, bullfinch, Puerto Rican owl and loggerhead kingbird. Todies and bananaquits maintained territories throughout the year.

With the exception of migrants and nocturnal birds, Kepler and Kepler (1970) compared the diversity and density of the avifauna in the Luquillo Experimental Forest with that in the Guánica Forest, a dry coastal forest (table 96). Both diversity and total density were significantly greater in Guánica. Twenty-two of the 38 birds observed in Guánica did not occur in the Luquillo Experimental Forest. However, only 6 of the 18 in the Luquillo Experimental Forest were absent from Guánica. Only four were considered to be obligate rain forest birds. Kepler and Kepler (1970) suggested that this may be a result of the larger number of greater proximity of xeric source areas as opposed to mesic source areas.

The life history of the Puerto Rican tody (*Todus mexicanus*) was studied and populations in the Luquillo Experimental Forest and Guánica Forest compared (Kepler and Kepler 1970). In the Luquillo Experimental Forest, highest densities of todies were found in the tabonuco and colorado forests where the bird nests in burrows constructed in earth banks. Lowest densities were in the palm and dwarf forests where these banks, if found, are hard, rock-like and difficult to penetrate. Feeding habitats, reproductive activity, nesting habits and territoriality were also examined. Greater nest failure occurred in the Luquillo Forest than in Guánica (fig. 85). The greater concentration of introduced mammals may be the

principal cause of the high nest failure (Kepler and Kepler 1970).

Originally found throughout the island, the Puerto Rican parrot (*Amazona vittata*) is now included on the federal Endangered Species List. Thousands were present in the 1930's, but by the 1950's Rodriguez-Vidal (1959) reported counts of only 200 birds. By 1966 the population had declined to about 15 and became restricted in range to the Luquillo Mountains (Recher and Recher 1966). This dramatic decrease stimulated intense efforts in 1968 by the Endangered Species Program of the Fish and Wildlife Service, in cooperation with the U.S. Forest Service, the World Wildlife Fund, and the Commonwealth of Puerto Rico, to study the parrot in an attempt to save it from its predicted extinction. An aviary was constructed in 1973 in the Luquillo Experimental Forest and studies have been conducted on both captive and wild birds. Presently 15 birds are studied in captivity and the wild population is estimated to be close to 30. Reasons for the decrease throughout the island included reduction of nesting sites by deforestation, as well as hunting and capture. Despite protection of the parrot's last refuge since 1918, the Luquillo Experimental Forest population continued to decline until 1971 (fig. 86). Reasons for this continued decline have now been narrowed to predation by the red-tailed hawk (*Buteo jamaicensis*), the Puerto Rican boa, feral cats, parasitism of young by botfly larvae (*Philornis pici*), destruction of nests and eggs by the pearly-eyed thrasher (*Margarops fuscatus*) and breeding failure by most individuals due to a scarcity of good nesting sites. (Snyder 1978). The parrot nests in deep, dry natural cavities of the palo colorado. Nest site scarcity has resulted from the fell-

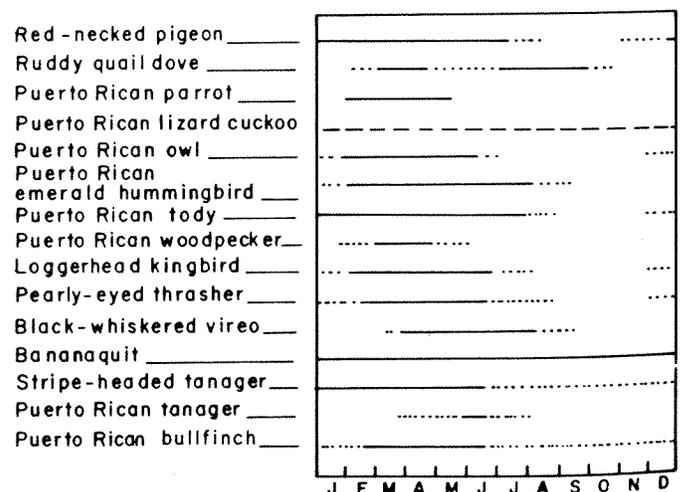


Figure 84.—Breeding seasons of some birds found in the Luquillo Experimental Forest (Recher 1970).

Table 94.—Composition of the avifauna at El Verde, given as individuals per 40 ha (Recher 1970)

Species [§]	March–April, 1964		August, 1964		December, 1964		April–May, 1965		May, 1966	
	Indiv.	Ind./40	Indiv.	Ind./40	Indiv.	Ind./40	Indiv.	Ind./40	Indiv.	Ind./40
Red-necked pigeon	4.0	16	*	*	*	*	3.0	12	3.0	12
Ruddy quail dove	6.0	24	10–12	40–48	15.0	60	5.0	20	4.0	16
Puerto Rican parrot	†	*	†	*	†	*	†	*	†	*
Puerto Rican screech owl	†	*	*	*	1.0	4	1.0	4	†	*
Puerto Rican lizard cuckoo	1.0	4	1.0	4	0.5	2	0.5	2	1.0	4
Puerto Rican emerald hummingbird	4.0	16	4.0	16	*	*	4.0	16	4.0	16
Puerto Rican tody	19.0	76	22.0	88	19.0	76	20.0	80	22.0	88
Puerto Rican woodpecker	0.5	2	3.0	12	3.0	12	1.0	4	1.0	4
Loggerhead kingbird	†	†	†	†	1.0	4	†	†	†	†
Pearly-eyed thrasher	12.0	48	11.0	44	*	*	16.0	64	6.0	24
Bananaquit	135.0	540	117.0	468	122.0	488	121.0	484	89.0	356
Black-whiskered vireo	34.0	135	16.0	64	†	†	30.0	120	18.0	72
Stripe-headed tanager	2.0	8	2.0	8	2.0	8	2.0	8	2.0	8
Puerto Rican tanager	7.0	28	6.0	24	7.0	28	10.5	42	8.0	32
Puerto Rican bullfinch	6.0	24	*	*	*	*	8.0	32	2.0	8
Total	229.5	918	189.0	756	168.5	674	221.0	884	130.0	640.0

*No estimate possible because of insufficient data.

†Not recorded from census area but seen in adjacent areas.

‡Not present.

§For Latin names, see table 96 (Puerto Rican screech owl = *Otus nudipes*).

Table 95.—Composition of the avifauna at Mt. Britton, given as individuals and as individuals per 40 ha (Recher 1970)

Species [§]	March–April, 1964		August, 1964		December, 1964		May, 1965		May, 1966	
	Indiv.	Ind./40	Indiv.	Ind./40	Indiv.	Ind./40	Indiv.	Ind./40	Indiv.	Ind./40
Red-necked pigeon	0.25	3	*	*	†	†	0.25	3	0.25	3
Ruddy quail dove	*	*	*	*	*	*	*	*	*	*
Puerto Rican parrot	†	†	*	*	*	*	†	†	†	†
Puerto Rican screech owl	†	†	†	†	†	†	†	†	†	†
Puerto Rican lizard cuckoo	†	†	†	†	†	†	†	†	†	†
Puerto Rican emerald hummingbird	1.0	11	1.0	11	1.0	11	1.0	11	†	†
Puerto Rican tody	5.0	56	5.0	56	5.0	56	5.0	56	5.0	56
Puerto Rican woodpecker	†	†	†	†	†	†	0.25	3	†	†
Loggerhead kingbird	*	*	*	*	*	*	*	*	*	*
Pearly-eyed thrasher	4.0	44	†	†	†	†	6.0	67	4.0	44
Bananaquit	53.0	588	47.0	522	26.0	289	35.0	389	34.0	378
Black-whiskered vireo	*	*	*	*	*	*	*	*	*	*
Stripe-headed tanager	†	†	0.5	6	0.5	6	0.5	6	0.5	6
Puerto Rican tanager	2.0	22	2.0	22	2.0	22	2.0	22	2.0	22
Puerto Rican bullfinch	4.0	44	†	†	4.0	44	5.0	56	5.0	56
Total	69.25	769	65.5	727	38.5	427	55.0	611	50.75	565

*Not present.

†Not recorded from census area but seen in adjacent areas.

‡No estimate possible because of insufficient data.

§For Latin names see table 96 (Puerto Rican screech owl = *Otus nudipes*)

ing of large colorados for charcoal production, hurricane related death of large colorados, and destruction of nest holes by honeybees and collectors of young birds. Construction of artificial nest sites and counteraction against the pearly-eyed thrasher have, in recent years, succeeded in successful breeding and stabilization of the population. Efforts to counteract the pearly-eyed thrasher have included provision of alternate, more favorable nest sites, manipulation of parrot nest sites to exclude thrashers, artificial incubation of parrot eggs, and direct guarding of nests.

Mammals

With the exception of an endemic bat fauna (Anthony 1925, 1926; Starrett 1962), mammals found in the Luquillo Experimental Forest have been introduced and have subsequently become widespread, replacing the few original, although now extinct, native ground mammals. Feral cats (*Felis catus*), the roof rat (*Rattus rattus*), the wharf rat (*Rattus norvegicus*), and the mongoose (*Herpestes javanicus auropunctatus*) are all presently common in forested areas, (table 93). First introduced to control the Puerto Rican boa, the mongoose is now a common and often problematic predator. Population studies of the roof rat estimate 40 rats/ha in the El Verde

area. The rat survival was relatively low despite the small number of predators, primarily the mongoose, observed during the study (fig. 87).

Little work has been done with the endemic bat fauna of either the Luquillo Mountains or of Puerto Rico. Tamsitt and Valdivieso (1970) collected four species (table 92), all of the family Phyllostomidae, from El Verde and identified ectoparasites found on them. One species, *Stenoderma rufum* (red fig-eating bat), previously reported as extinct (Anthony 1925), was captured alive for the first time in Puerto Rico. Tamsitt and Valdivieso (1966) describe this bat in detail.

Three species of bats are frugivorous and one nec-tivorous (*Monophyllus redmanni*). No insectivorous bats have been collected to date in the Forest; however, Tamsitt and Valdivieso (1970) state that with more intensive collecting, one more frugivorous and six insectivorous bat species may be captured. Numerous opportunities for continued research with bat fauna exist as little is known concerning reproductive behavior, feeding habits, population dynamics, or seasonality, nor the effect of the multitude of introduced fruit crops on population densities and species composition.

Molluscs

An additional component of the fauna of the Luquillo Experimental Forest are the several species of land snails (table 92). Golley (1960) reported *Nenia*

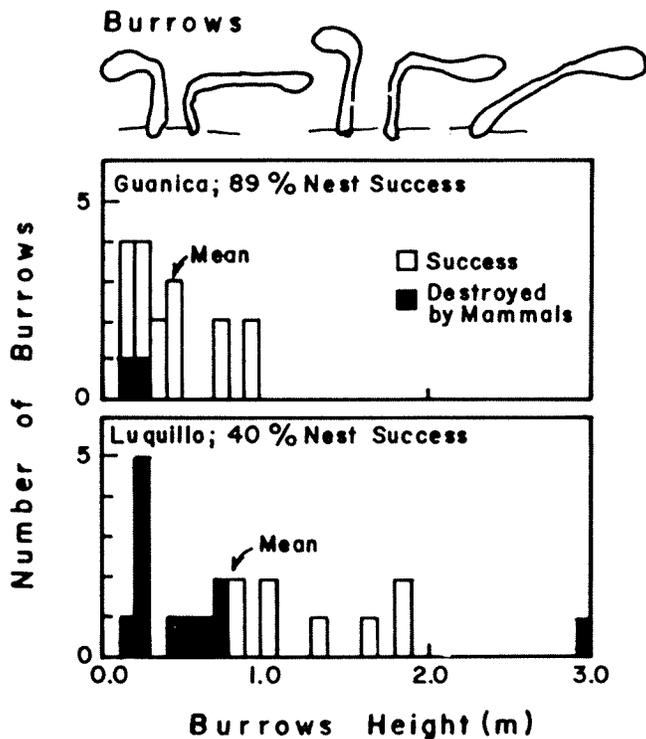


Figure 85.—Nesting success of Puerto Rican tody (*Todus mexicanus*) in the Luquillo Experimental Forest and Guánica Forest (Kepler and Kepler 1970).

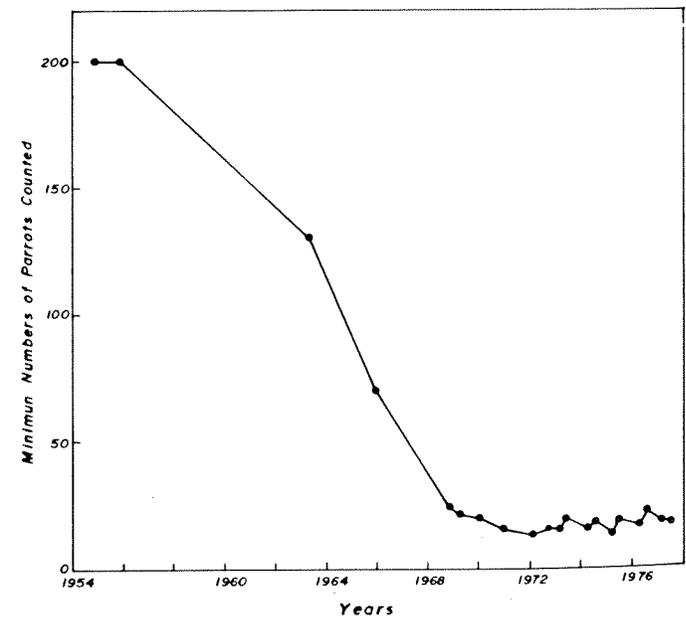


Figure 86.—Change in parrot population (as measured by the minimum number of parrots counted) with time (Snyder 1978).

Table 96.—Composite counts for seven census tracts in two Puerto Rican forests (Kepler and Kepler 1970)

Species	Latin names	Forest Luquillo	Forest Guanica
1. Turkey vulture	<i>Cathartes aura</i>		2
2. Sharp-shinned hawk	<i>Accipiter striatus</i>	P*	
3. Red-tailed hawk	<i>Buteo jamaicensis</i>	4	1
4. Broad-winged hawk	<i>Buteo platypterus</i>	P	
5. Sparrow hawk	<i>Falco sparverius</i>		2
6. Red-necked pigeon	<i>Columba squamosa</i>	49	
7. Zenaida dove	<i>Zenaida aurita</i>		149
8. Ground dove	<i>Columbigallina passerina</i>		356
9. Key West quail dove	<i>Geotrygon chrysia</i>		3
10. Ruddy quail dove	<i>Geotrygon montana</i>	6	10
	<i>Geotrygon sp</i>		2
11. Puerto Rican parrot	<i>Amazona vittata</i>	3	
12. Mangrove cuckoo	<i>Coccyzus minor</i>		36
13. Yellow-billed cuckoo	<i>Coccyzus americanus</i>		25
14. Puerto Rican lizard cuckoo	<i>Saurothera vieilloti</i>	1	12
15. Smooth-billed ani	<i>Crotophaga ani</i>		5
16. Black swift	<i>Cypseloides niger</i>	6	
17. Puerto Rican emerald hummingbird	<i>Chlorostilbon maugaeus</i>	10	3
18. Antillean mango hummingbird	<i>Anthracothorax dominicus</i>		26
19. Green mango hummingbird	<i>Anthracothorax viridis</i>	P*	
20. Puerto Rican tody	<i>Todus mexicanus</i>	40	82
21. Puerto Rican woodpecker	<i>Melanerpes portoricensis</i>	12	51
22. Gray kingbird	<i>Tyrannus dominicensis</i>		55
23. Loggerhead kingbird	<i>Tyrannus caudifasciatus</i>	P*	1
24. Stolid flycatcher	<i>Myiarchus stolidus</i>		65
25. Lesser Antillean pewee	<i>Contopus latirostris</i>		1
26. Cave swallow	<i>Petrochelidon fulva</i>	P*	26
27. Carribean martin	<i>Progne dominicensis</i>		9
28. Mockingbird	<i>Mimus polyglottos</i>		16
29. Pearly-eyed thrasher	<i>Margarops fuscatus</i>	41	10
30. Red-legged thrush	<i>Mimocichla plumbea</i>	1	6
31. Puerto Rican vireo	<i>Vireo latimeri</i>		63
32. Black-whiskered vireo	<i>Virco altiloquus</i>	13	79
33. Bananaquit	<i>Coereba flaveola</i>	245	161
34. Adelaide's warbler	<i>Dendroica adelaidae</i>		218
35. Yellow-shouldered blackbird	<i>Agelaius xanthomus</i>		3
36. Black-cowled oriole	<i>Icterus dominicensis</i>	P*	3
37. Troupial	<i>Icterus icterus</i>		51
38. Greater Antillean grackle	<i>Quiscalus niger</i>		1
39. Glossy cowbird	<i>Molothrus bonariensis</i>		4
40. Blue-hooded euphonia	<i>Tanagra musica</i>	2	3
41. Stripe-headed tanager	<i>Spindalis zena</i>	P*	5
42. Puerto Rican tanager	<i>Nesospingus speculiferus</i>	75	
43. Yellow-faced grassquit	<i>Tiaris olivacea</i>	9	12
44. Black-faced grassquit	<i>Tiaris bicolor</i>	1	69
	<i>Tiaris sp</i>		5
45. Puerto Rican bullfinch	<i>Loxigilla portoricensis</i>	29	190
Total individuals		547	1821
Total number of species		18	38
Birds/km		57	190

*P, species known to be present, but not observed on census.

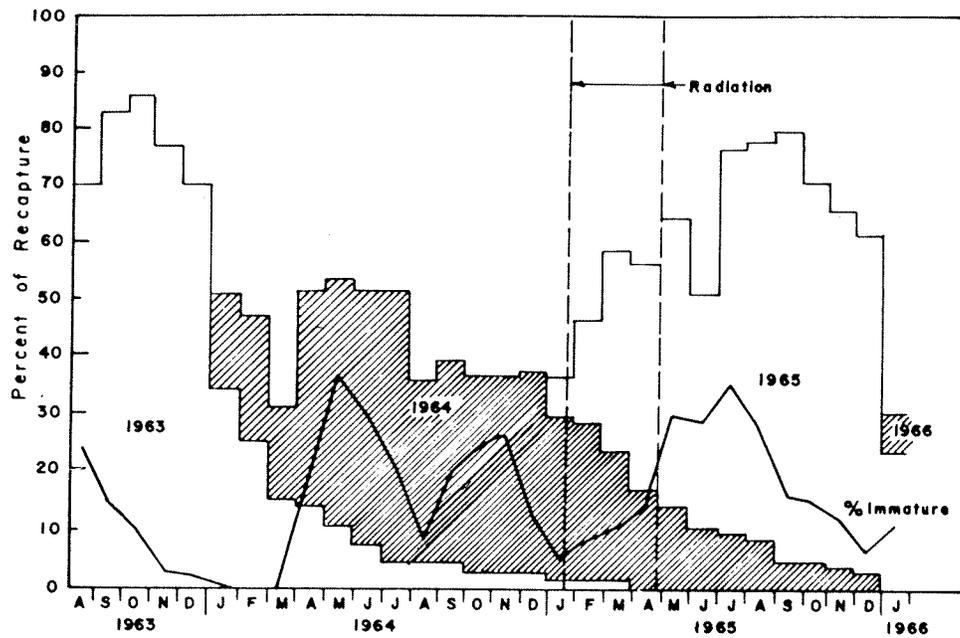


Figure 87.—Survival patterns for annual classes of rats in the tabonuco forest at El Verde (Weinbren et al. 1970).

tridens to be the most abundant snail on ridges and *Caracollus caracola* in ravines. *Megalomostoma croceum* was most abundant in leaf litter. Average number of snails on the ground was 0.4/m² and on trees 1.8/m². Population studies of *C. caracola*, the most conspicuous snail, showed it to be common in moist mountain and lowland forests, but in open disturbed areas and roadsides it is replaced by *C. marginalla* and *Polydontes lima* (Heatwole et al. 1970). Two less abundant species, *P. acutangula*, frequenting the canopy and open area, and *P. luquillensis*, ecologically similar to *C. caracola*, are restricted to the rain forest in eastern Puerto Rico. During May, when maximum growth of the Caracollus snail occurs, the population had relatively few juvenile snails, and approximately half of the population consisted of adults (fig. 88). The population during the remainder of the year was rather evenly distributed. Population estimates suggested an average density of 0.12/m². Relatively little is known of the reproductive behavior of this snail.

Aquatic Fauna

Gifford and Cole (1970) conducted preliminary surveys of the decapod fauna of the Espiritu Santo River System and investigated aspects of their ecology and distribution. A recent limnological survey of the Espiritu Santo River System (c.f. fig. 26) reported nine decapod crustaceans, eight species of shrimp, one species of crab, seven orders of drifting invertebrate larvae and one species of fish from forested areas of the watershed (Bhajan et al. 1980). Two ad-

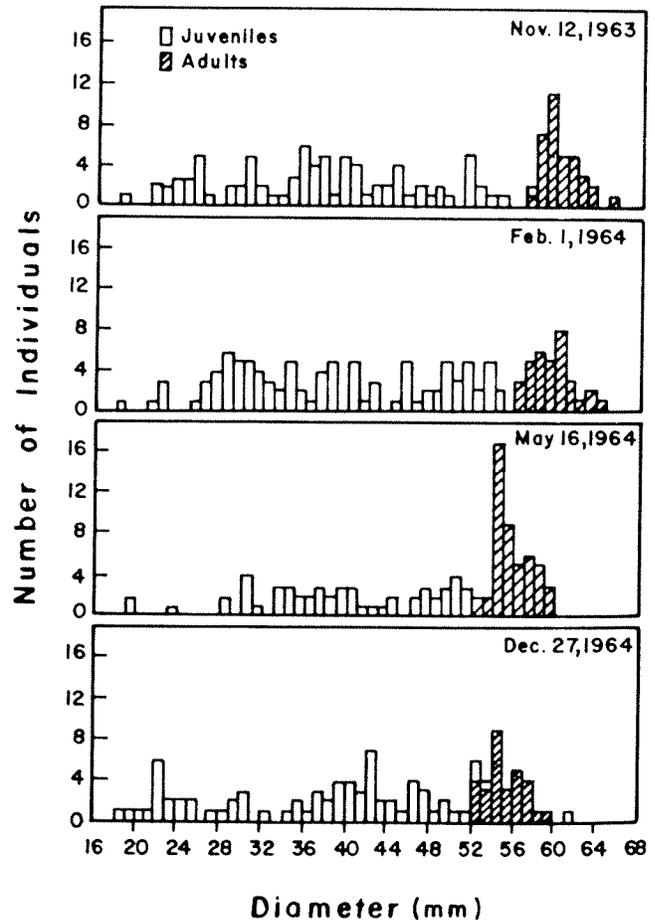


Figure 88.—Population structure of *Caracollus caracola* at different times of the year in the tabonuco forest (Heatwole et al. 1970).

ditional species of freshwater fish may inhabit rivers at the lower fringes of the forest. The freshwater snail, *Neritina reclivata*, was present at lower elevations and the extreme shell erosion is presently being investigated. These species are listed in table 92 and their altitudinal ranges illustrated in figure 89. Salinity bioassays conducted during the above limnological survey (Bhajan et al. 1980) verify existence of an estuarine larval phase in several species of freshwater shrimp. For this reason, and because of rapidly changing conditions in estuaries, the DNR has listed seven of these species, commercial on a seasonal basis, as vulnerable.

Canals (1977) found *Macrobrachium crenulatum* in the Espiritu Santo River for the first time in Puerto Rico and discussed aspects of its ecology (Canals 1979). This species is the most abundant member of the Palaemonidae family, and is most common at middle elevations (220 to 440 m). August appeared to be the peak breeding season and the existence of an estuarine larval phase was again substantiated. Villamil and Clements (1976) described the ecology of four shrimp species, (*Atya lanipes*, *A. innocuous*,

Macrobrachium heterochirus and *Xiphocaris elongata*) found in the upper Espiritu Santo River, including distribution, relationship to physical and chemical factors, feeding habits, habitat description, and comparison of physical characteristics of the species. Intraspecific habitat selection in *Atya lanipes*, a filter feeder, is illustrated in figure 90. Males were found predominantly in high-flow areas where the substrate was boulders, whereas females were more frequent in low-flow areas with rubble and gravel substrates.

Epilobocera sinuatifrons, the only fresh water crab in Puerto Rico, utilizes both land, where they borrow in stream banks, and aquatic habitats, to which the young are restricted. The species feeds upon any decaying material.

Sicydium plumieri, the gobiid fish with extreme sexual color dimorphism, has also been reported to have a marine phase. Eggs are laid under rocks in freshwater from May to October and are washed to sea during heavy rains. Larvae return one month later to migrate upstream. The post-larvae or seti are a food delicacy, caught as they enter the river mouth

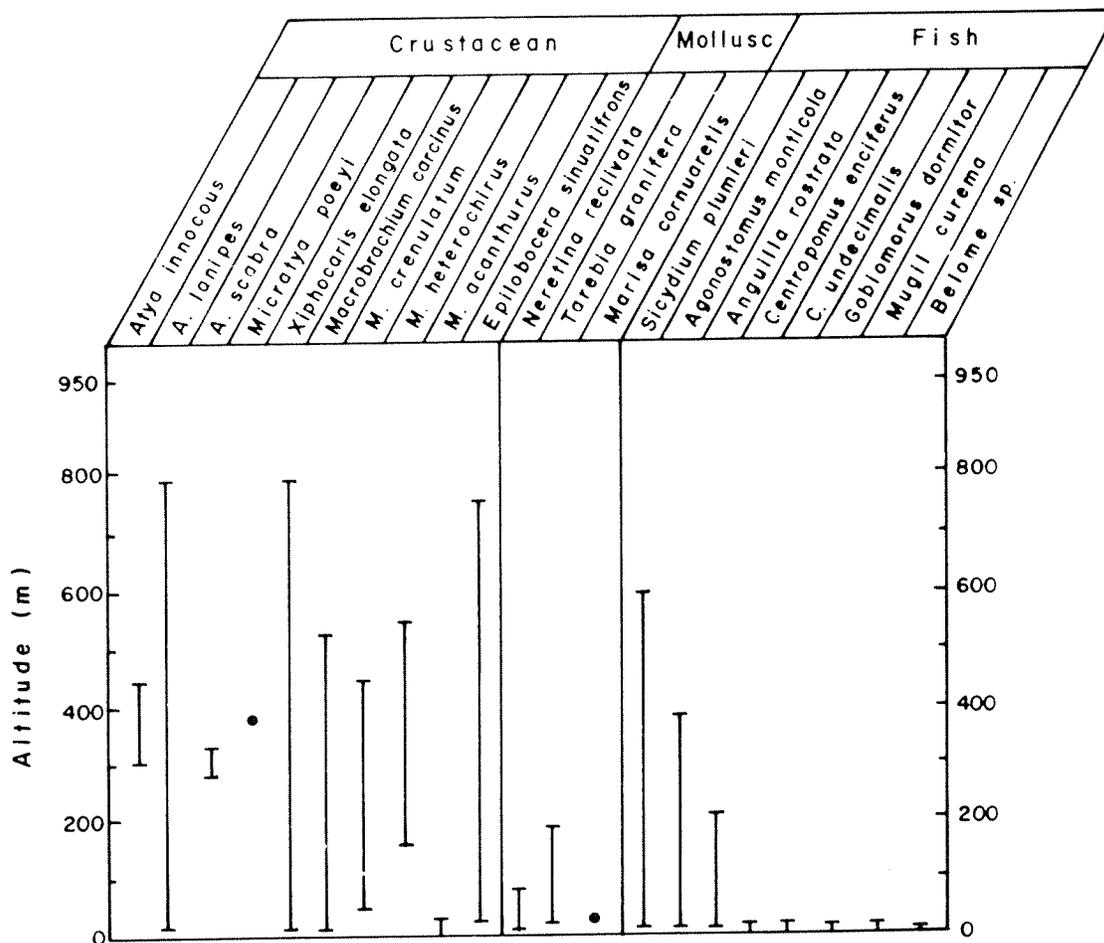


Figure 89.—Altitudinal distribution of the fauna of the Espiritu Santo River (Bhajan et al. 1980).

in a massive red-silver ball. During the breeding season the male becomes an iridescent blue-green color (Erdman 1961).

DISTURBANCES

The history of disturbance in the Luquillo Experimental Forest is well known, although ecosystem responses are not well studied for each type of disturbance. Yet, frequent human-related and natural disturbances to the forest have created a mosaic of areas in various stages of succession. This mosaic nature of the forest is apparent even from a distance, due to the white-silver undersides of the leaves of *Cecropia*, the principal woody invader of canopy gaps. A list of the most significant disturbances to the Luquillo Experimental Forest includes the following human-induced and natural events:

- early cutting for wood products and agricultural uses (prior to 1917);
- agricultural use of land;
- experimental manipulations including cutting, herbicides, and ionizing radiation;
- miscellaneous use of the land including roads, recreational areas, transmission towers, etc;
- accidents such as an airplane accident in the dwarf forest;

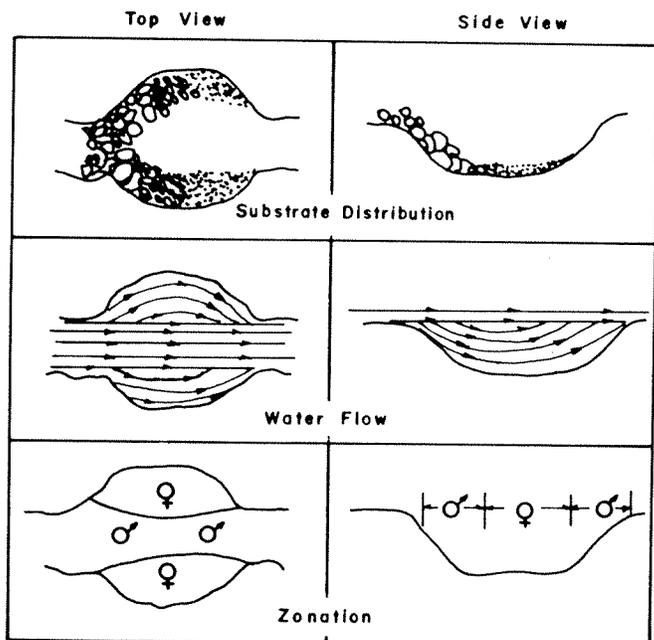


Figure 90.—Patterns of water flow and substrate distribution in a typical pool in the Espiritu Santo River and their relationship to habitat selection by *Atya lanipes* (Villamil and Clements 1976).

- landslides caused by poor use of land or by natural forces; and
- hurricanes or other unusual high wind or high rainfall events.

The following discussion focuses mostly on the forest's response to ionizing radiation because this is the best documented of all the disturbances. The response of the dwarf forest to accidental disturbance is discussed in the corresponding earlier section. Responses to other disturbances are discussed briefly after the discussion on radiation effects.

Irradiation Damage and Recovery

The ecological effects of three months of irradiation (February-April 1965) with 20,000 curies of cesium at El Verde are discussed in detail in Section D of Odum and Pigeon (1970). The affected area was approximately 80 m in diameter. The most obvious effect was defoliation which continued for three months after the radiation source was removed. This caused a decrease in canopy optical density (fig. 91). Microclimatic changes that occurred upon the creation of the canopy gap and their gradients with distance from the center of disturbance are illustrated in figures 92, 93, and 94. Light intensity and air temperature increased and relative humidity decreased. Soil temperature increased by as much as 7°C, creating a more vigorous environment for seeds and seedlings (McCormick 1970).

In response to these and other environmental changes, a seedling explosion occurred in the forest gap created by radiation. Two species were especially prolific in early regeneration *Palicourea riparia*, a shrub, and *Phytolacca icosandra*, a weedy roadside plant. Autecological studies of the latter species indi-

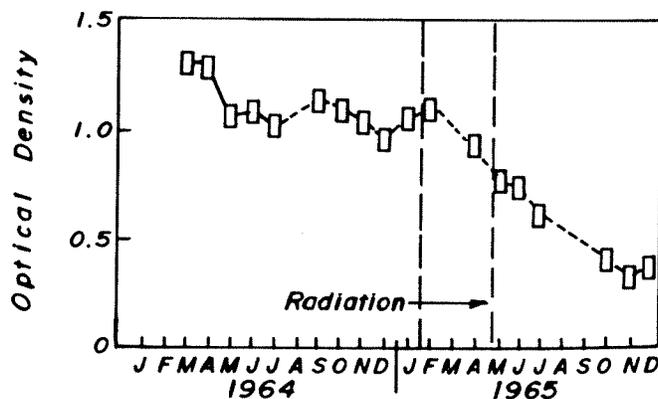


Figure 91.—Monthly means of optical density in the middle of the day at the Radiation Center. Squares indicate one standard error of the mean. (Odum et al. 1970).

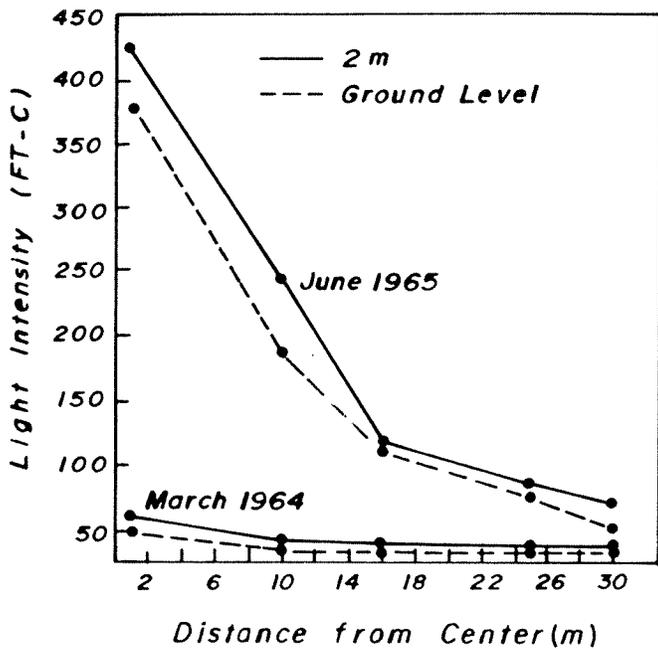


Figure 92.—Light-intensity gradients in the Radiation Center before and after irradiation. Each point is an average of measurements taken along eight different compass bearings (McCormick 1970).

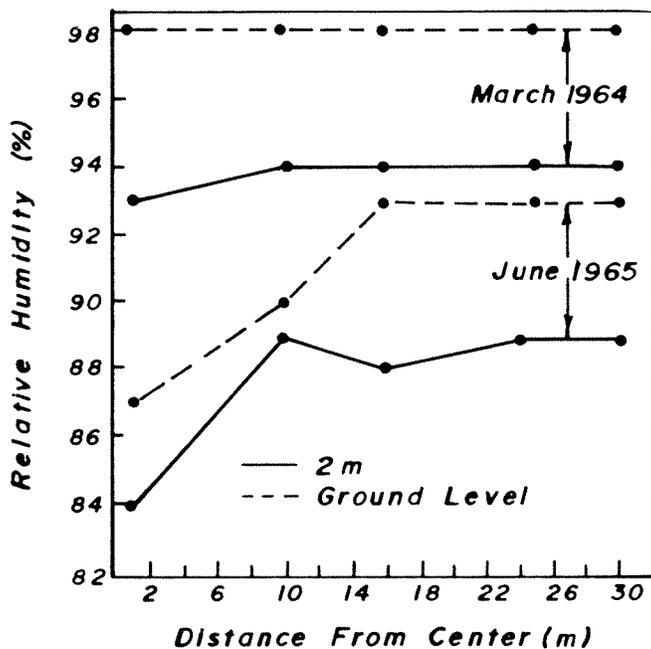


Figure 93.—Relative humidity gradients in the Radiation Center before and after irradiation. Each point is an average of measurements taken along eight different compass bearings (McCormick 1970).

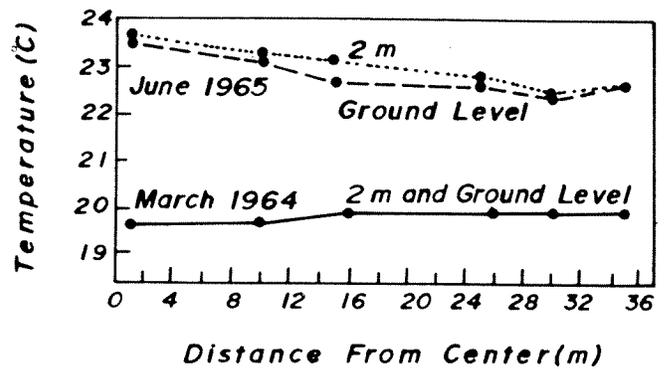


Figure 94.—Temperature gradients in the Radiation Center before and after irradiation. Each point is an average of measurements taken along eight different compass bearings (McCormick 1970).

cated that germination of its bird dispersed seeds was increased by mechanical and acid scarification and elevated soil temperature, conditions which are likely to occur upon the opening of the canopy (Edmisten 1970b). Light, however, did not significantly affect the germination of this species (Bell 1970). The high radiation resistance discovered in *Palicourea riparia* may be related to the small size of chromosomes, polyploidy, and inherent high frequency of cytological abnormalities (Venator and Koo 1970).

The ability of *Palicourea* to carry on photosynthesis at very low light intensities found within the forest make it a predominant understory species, but its capacity to increase germination, growth and photosynthesis in openings enable it to act as a "gap opportunist" (Lebrón 1977).

Light stimulated germination by three more species, *Cecropia peltata*, *Didymopanax morototoni*, and *Psychotria berteriana*, is illustrated in table 97. Both *Cecropia* and *Didymopanax* are common woody successional species which quickly establish a vertical structure by means of their rapid height growth. In contrast, germination of the climax dominant species, tabonuco, was found to be higher under shaded conditions.

Post-irradiation seedling population densities in irradiated, experimentally cut, and control center sites are compared in table 98. Frequent in forest openings are the woody species, *Alchornea*, *Cecropia*, *Didymopanax*, *Inga*, *Psychotria*, and *Tabebuia* and the vine, *Cissampelos*. The lower seedling density in the radiation center was probably a result of the slower opening of the canopy rather than an effect on the radiation itself. Immediately following irradiation, seedling diversity was significantly reduced (McCormick 1970).

Table 97.—Seedling emergence from forest soil placed in a clearing and within the forest (Bell 1970)

Species	Number of seedlings		Relative density in canopy, %*
	Clearing	Forest	
<i>Alchornea latifolia</i>	3	6	1.9
<i>Cecropia peltata</i>	271	8	4.6
<i>Cissampelos pareira</i>	1	1
<i>Didymopanax morototoni</i>	22	0	22
<i>Euterpe globosa</i> **	1	1	2
<i>Guettarda laevis</i>	4	3	7
<i>Linociera domingensis</i>	0	1	1
<i>Psychotria berteriana</i>	121	3	124
<i>Phytolacca icosandra</i>	19	11	30
<i>Paullinia pinnata</i>	0	1	1
<i>Palicourea riparia</i>	0	83	83
<i>Rajania cordata</i>	4	4	8
<i>Sapium laurocerasus</i>	2	0	2
Totals	448	122	570

*From R. F. Smith (1970).

†Percent of understory cover.

‡Percent of liana cover.

***Prestoea montana*.

Censuses of all plants within a 30 m radius of the source were conducted annually until 1969, and thereafter in 1971, 1973, 1975, and 1977. These data are presently being analyzed by the Center for Energy and Environmental Research. In general, the number of species increased, but the number of new individuals reached a peak two years after irradiation and since declined (table 99). The number of vines increased as did the total number of individuals. Initially, the relative density of primary species, such as tabonuco, decreased, but in later years their density began to increase (fig. 95a). In contrast, secondary species initially increased in relative density, but more recently a decreasing trend is appearing (fig. 95b). The same trend may be observed in understory primary and secondary species (fig. 96). Total number of sprouts increased through time. Ten years after disturbance, the forest appeared to be recovering from the damage (Lebrón 1977).

Both bryophytes (Steere 1970) and crustose lichens (Gannutz 1970) were found to be more resistant to radiation than were higher plants. Ferns were unexpectedly resistant despite their high nuclear volume and chromosome number.

Tabonuco trees close to the radiation center (0–25 m and received more than 7,000 r of radiation) grew at less than half their normal rate during the post-irradiation period (fig. 97e). Other slower growing species within 25 m of the radiation source temporarily terminated growth shortly after radiation began, but returned to near-normal growth during

the post-irradiation period (fig. 97b–d). *Cecropia* on the other hand appeared to have greater growth rates in the post-irradiation period than during the pre-irradiation period (fig. 97a).

The earlier soil section contains some discussion on the impact of radiation on soil and organisms.

Herbicide and Experimental Cutting Damage and Recovery

Recovery following irradiation may be compared to that following the application of various types and strengths of herbicides (Dowley and Tschirley 1970).

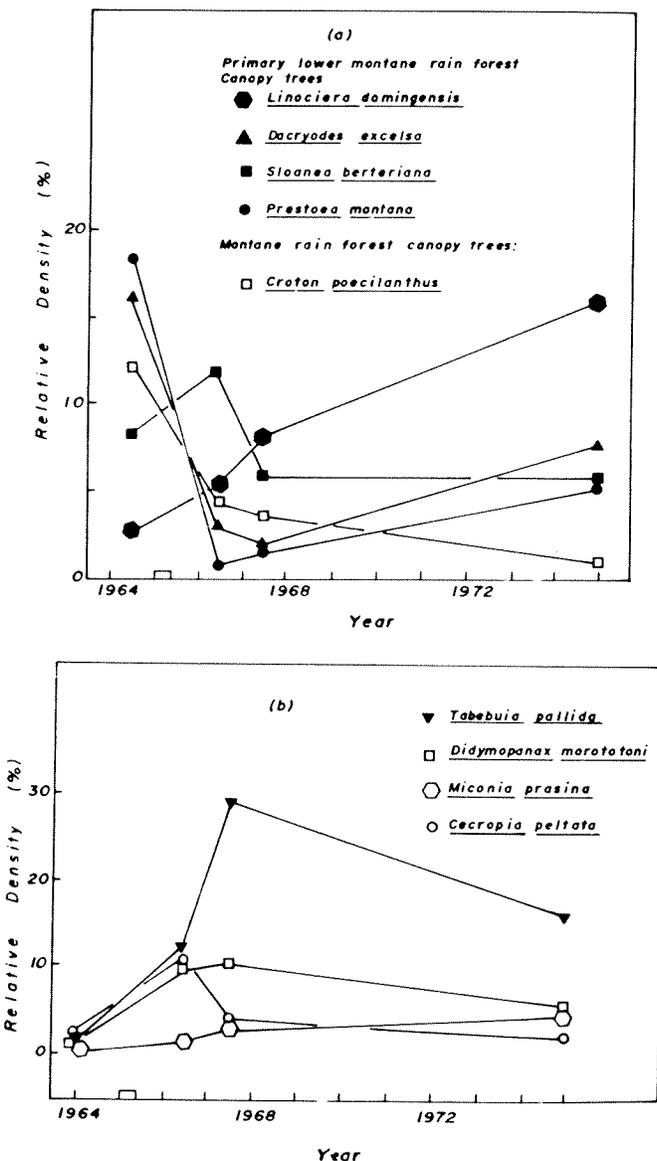


Figure 95.—Relative density of (a) primary lower montane rain forest (tabonuco) canopy trees and (b) secondary lower montane rain forest canopy trees in the years following irradiation (Lebrón 1977).

Table 98.—Comparison of populations of woody seedlings in the 3.2 m radius plots at El Verde (Duke 1970)

Genus	Type*	No. of individuals			Percentage of total individuals		
		North cut center	Radiation center	South control center	North cut center	Radiation center	South control center
<i>Alchornea</i>	P	7	6	0	2	8	0
<i>Andira</i>	C	17	0	0	6	0	0
<i>Byrsonima</i>	P	3	0	0	1	0	0
<i>Casearia</i>	P	1	0	0	1	0	0
<i>Cecropia</i>	P	56	4	0	19	5	0
<i>Cissampelos</i>	P	5	1	0	2	1	0
<i>Citrus</i>	P	0	0	4	0	0	5
<i>Clusia</i>	P	0	1	0	0	1	0
<i>Cordia</i>	P	0	0	1	0	0	1
<i>Croton</i>	P	0	1	0	0	1	0
<i>Dacryodes</i>	C	3	0	1	1	0	1
<i>Didymopanax</i>	P	13	2	0	5	3	0
<i>Dioscorea</i>	C	0	0	2	0	0	3
<i>Drypetes</i>	P	4	0	14	1	0	18
<i>Eugenia</i>	C	10	0	0	3	0	0
<i>Hirtella</i>	C	0	0	29	0	0	37
<i>Inga</i>	C	2	1	0	1	1	0
<i>Linociera</i>	P	26	1	5	9	1	6
<i>Manilkara</i>	P	5	0	0	19	0	0
<i>Matayba</i>	C	0	2	1	0	3	1
<i>Miconia</i>	P	0	0	1	0	0	1
<i>Nectandra</i>	C	9	0	0	3	0	0
<i>Ocotea</i>	C	2	0	0	1	0	0
<i>Ormosia</i>	C	0	0	1	0	0	1
<i>Piper</i>	P	4	0	0	1	0	0
<i>Prestoea</i>	C	29	0	4	10	0	5
<i>Psychotria</i>	P	88	7	1	31	9	1
<i>Rourea</i>	C	3	3	9	1	4	11
<i>Securidaca</i>	C	0	0	4	0	0	5
<i>Sloanea</i>	P	0	0	2	0	0	3
<i>Smilax</i>	C	0	3	0	0	4	0
<i>Swietenia</i>	C	1	0	0	1	0	0
<i>Tabebuia</i>	P	0	45	0	0	58	0
Total genera		20	13	15			
Total individuals		288	77	79			
Cryptocotylar genera (%)		45	38	53			
Cryptocotylar individuals (%)		26	12	65			

*P, phanerocotylar; C, cryptocotylar.

Recovery resembled that in the radiation center, except that it lagged somewhat due to toxic effects of the herbicides on seed storage and shoot regeneration. Jordan (1967) compared species diversity in the irradiated, herbicided and cut areas. Highest values were reported for the cut area (north cut center), intermediate for the radiation site, and lowest in the herbicide plots, suggesting that herbicide treatment may have created the greatest stress.

Studies in the cut area revealed the normal mechanisms of repair which operate following the types of natural disturbances that occur so frequently in the Luquillo Mountains e.g., tree falls,

storm damage, landslides due to saturated soils, and hurricane damage. The mechanisms included explosive germination of stored seed, enhanced growth of older seedlings and saplings already present in response to increased light, germination from newly transported seed (*Phytolacca icosandra*), and rapid shoot growth from regeneration of root systems. The section on long-term observations on forest dynamics contains a discussion of forest growth following 50% reduction of basal area.

Although faunal species composition was altered somewhat with the invasion of *Anolis cristatellus*, a species more characteristic of lowland and sunnier

areas, arthropod and animal populations were not significantly affected by these stressors. Grazing activity increased only slightly, but was high on the early successional species (Odum 1970b). The continuous natural disturbance which occurs in these mountains has apparently enabled the evolution of rapid recovery mechanisms such as the re-invasion of sites by some species and the great resistance of others.

Although microbial activity increased following the influx of leaf litter, mineral loss from the system did not accelerate. Lateral flows of energy in the form of seed, rain, and animal movement contributed to rapid regeneration.

Hurricanes

Wadsworth (1951) estimated that hurricanes occur on the average once every 10 years in Puerto Rico. Wadsworth and Englerth (1959) found that emergent and isolated trees were the most susceptible to overturn. In a comparison of the tabonuco forests of Puerto Rico and Dominica to tropical rain forests of the mainland, the island forests were found to have physiognomic characteristics which may be advantageous in the minimization of hurricane damage. On the islands, the canopy is generally more even and emergents, with large round crowns, found in lowland forest without hurricane activity, are absent. This even canopy may be maintained by continuous loss of limbs from large trees so that many trees die in place (fig. 98). Crow (1980) suggested that frequent hurricanes and consequent creation of light gaps may help to maintain the high species diversity found in the tabonuco forest. The more recent severe hurricane of 1979 may provide an excellent opportunity to test this hypothesis.

Table 99.—Regeneration in the radiation center following irradiation at El Verde (Lebrón 1977)

	1966	1967	1975
Number of new individuals	3211	6590	5912
Percent of total	61.21	76.00	50.36
Number of sprouts	643	905	967
Percent of total	12.26	10.44	8.24
Number of vines: (Ind.)	568	789	2252
Total number of individuals	5246	8671	11739
Overall center density: (# ind./m ²)	7.76	12.83	17.37
Total number of species	97	121	137

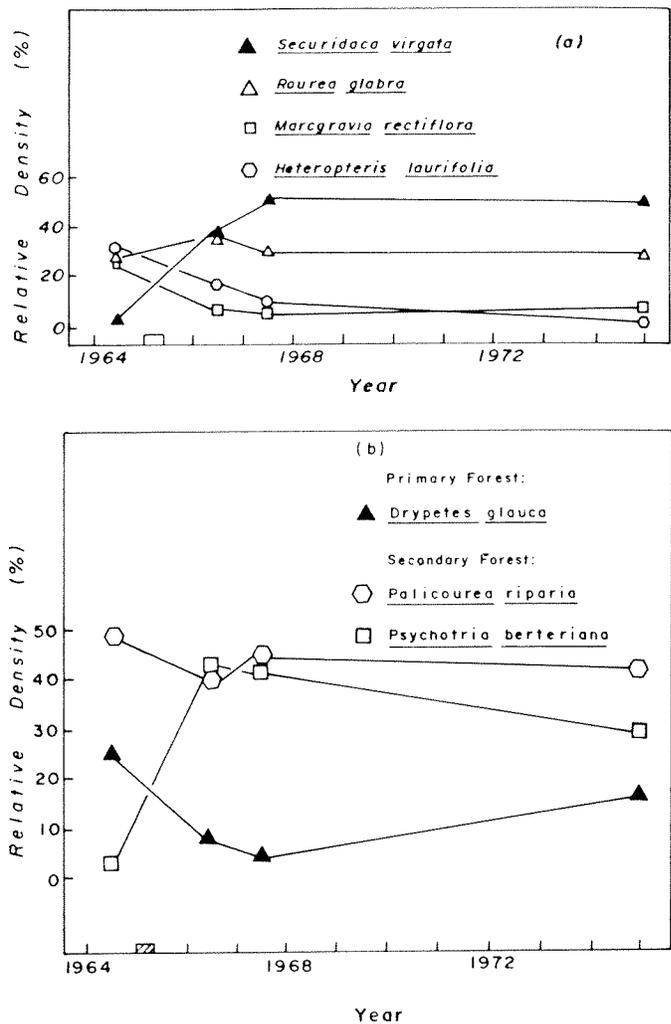


Figure 96.—Relative density of (a) climbers and (b) primary and secondary understory species following irradiation at El Verde (Lebrón 1977).

CONCLUSION

The ultimate objective of ecological research is understanding natural ecosystem function. What drives ecosystems? How do they cope with environmental uncertainty? Are these general patterns of ecosystem response that repeat themselves regardless of ecosystem type or environmental conditions? These are questions that we cannot resolve, but which we strive to answer because in their solution resides considerable advantage in our efforts to manipulate ecosystems for the benefit of humans. The Luquillo Mountains are an ideal place to study these problems because they contain a mosaic of ecosystems whose distributions coincide with measurable environmental changes.

We know, for example, that the dwarf forest is closely associated with an environment that can be

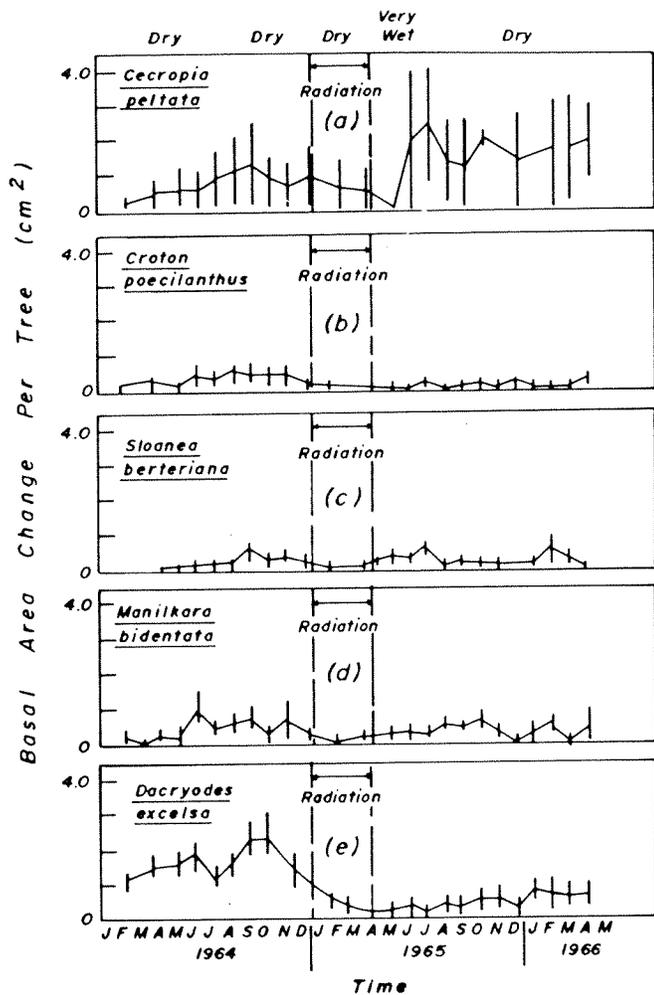


Figure 97.—Effects of radiation on tree growth (Murphy 1970). All trees were within 0–25m of the radiation source and received 7,000–1,000,000 r of radiation.

described as cloudy, very wet, relatively cool, in steep terrain, and extremely windy. However, within minutes these conditions may reverse; i.e. they can turn sunny, dry, warm and calm. Below the cloud condensation level most of the same species found in the dwarf forest develop a forest (described above as the colorado forest) with a taller canopy, larger and less coriaceous leaves, large diameter trees, and lower tree density. Regardless of altitude, monocultures of palms develop in places where the soils are waterlogged and anaerobic. Yet, in lower altitudes where the air is drier, cloudiness is less pervasive, rainfall is lower, and soils are deeper or well aerated, the tabonuco forest develops with great splendor. To an observer of this ecosystem mosaic the obvious conclusion is that the dwarf forest responds mainly to atmospheric conditions, the palm forest is an edaphic climax, and the colorado and tabonuco types reflect the normal difference associated in forests located at different elevations. While this interpretation supported by this literature review may be true,

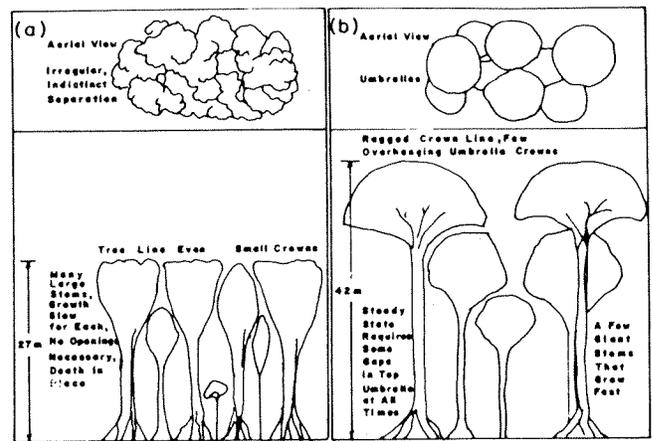


Figure 98.—Theoretical diagram of forest structure in relation to the hurricane factor showing differences in crown size, canopy-stem ratios, boundaries of crowns in aerial views, and the relative rates of photosynthetic contribution per stem growth. (a) Hurricane type (Dominica, Puerto Rico) (b) Lowland equatorial type (Costa Rica) (Odum 1970a).

it is incomplete. More specific answers about ecosystem response to external forces are needed. Unfortunately, reviewing the data base one discovers that the existing information gaps create more questions than can be answered. Formulating these new questions will be the task of the remainder of this section.

Forcing Functions

The section on climate has summarized trends in the external factors that converge on the Luquillo Mountains. Data sets are not comprehensive, nor do they have enough continuity to allow time series analysis. Temperature records are surprisingly poor and other factors such as atmospheric inputs of elements and dust have hardly been measured.

In fig. 46 Odum (1970b) calculated the relative energy contribution of energy sources to the tabonuco forest. Their ranking in terms of heat energy is sunlight, dry air, rainfall, wind, CO₂, and rocks. The diagram provides an idea of where in the tabonuco system these energies interact. Are their magnitudes and interactions the same for the four ecosystems of the Luquillo Mountains? The answer is obviously no. We do not know enough yet to quantify these differences.

The gradient of forces converging on these mountains, however, poses serious problems to plants and animals. While temperatures never reach freezing, and rainfall and solar energy are abundant, these and other factors do show considerable variation in space and time. The climate sections describe diurnal, monthly, seasonal and annual patterns for all these factors. Yet, perhaps the most significant prob-

lem to organisms is rainfall. These forests receive an average rainfall that ranges between 245 and 400 cm annually, depending upon altitude. This water dissipates energy on surfaces and causes leaching of organic matter and elements vital to ecosystem function. Consequently, most of the adaptations of these ecosystems may be interpreted in terms of water or water-related factors. Another contingency that these forests must cope with is hurricanes which pass over the forest at long-term intervals causing severe structural and functional disruptions that may take up to 40 yr to repair. The response of the Luquillo Mountains forests to the problems of excess water and hurricanes is a vital concern.

Response To Water

The water that falls on the Luquillo Mountains originates in the sea where trade winds constantly pick up moisture and then discharge it orographically as described earlier. Water is used for plant growth, transpiration, and metabolic processes in both plants and animals. Water acts as a stimulus for phenological processes, provides buffering against sharp temperature changes, favors amphibians and reptiles who depend on moisture for gas exchange, and it generally acts as a catalyst to energy and matter cycling through the ecosystem. However, water also acts as a stressor on soil and leaves as it falls with considerable momentum. This fall of rain tears tissues and causes soil erosion. More significantly, water leaches minerals and organic matter downstream. Too much water in the soil creates anaerobic conditions which in turn create severe metabolic problems for roots. Too much moisture also results in a saturated atmosphere which inhibits evaporation. This, in turn, creates problems for trees whose transpiration is reduced. With reduced transpiration, transport of nutrients to leaves may decrease and so may growth and tree height (Odum 1970a).

The forests in the Luquillo Mountains are finely tuned to variations in moisture availability and contain numerous mechanisms and adaptations that minimize the negative effects of too much moisture, while taking advantage of the positive attributes of the available water. A number of examples of forest responses that take advantage of the presence of moisture are the following:

- Tree growth, seed germination, explosive seedling growth, leaf fall, flowering and fruiting are all synchronized to slight changes in rainfall, which was documented in El Verde (fig. 56).
- Bromeliads and other epiphytic organisms store water within their leaves and large and diverse populations of animals utilize these as habitats and for reproduction.

- Tap roots, abundance of deciduous species, and tree growth rings, which are normal responses to moisture seasonality, are not usual features in the forests of the Luquillo Mountains.

Adaptations that minimize the impacts of too much water are:

- Epiphytic coverage of surfaces increases with increasing moisture which in turn, contributes to an even distribution of through-fall by temporarily storing water and reducing its impact on other surfaces.
- Epiphytes also absorb nutrients from incoming waters and this contributes to a reduction in the loss of minerals to downstream ecosystems.
- Anatomical and morphological characteristics of plants growing at high elevations and low saturation deficits contribute to the increase in transpiration rates. For example, number and size of stomata increase with altitude.
- Where saturation deficits are high, anatomical and morphological characteristics of plants reduce water loss.
- Palms develop massive adventitious roots, laden with lenticels, that may contribute to root gas exchange in anaerobic soils.
- Surface and adventitious roots increase dramatically with increasing water logging of soils (figs. 36 and 40).
- Trees maintain epiphyte-laden old leaves for long time periods in spite of the low P/R ratio of these leaves. It appears that their role in mineral cycling and nutrient conservation has more selective advantages than their role as net organic matter producers.
- Forests have extensive root mats that are essentially mineral-tight.
- Plants flower for longer periods in the wetter sites and depend on insects and birds for pollination.

We know that excessive water causes a problem to these forests because mineral losses by leaching are significant (fig. 51). However, adaptations to prevent mineral losses must be effective because, in spite of a large amount of runoff, the forests at high altitudes lose less minerals in runoff than the forests downstream.

Response To Hurricanes

When a hurricane strikes these forests considerable amounts of structure are destroyed. In response, succession is fast, in part because the simple event of canopy opening triggers the germination of a considerable number of fast growing species that quickly cover the forest floor. The section on long-term forest dynamics, however, shows that, if all the changes

put in motion by the hurricane are taken into consideration, the repair of the forest may take four decades. This is the strongest evidence to support the idea that forest structure and function is driven by external events. That is, while forest organisms obviously develop close associations and slowly modify their environment over long periods of time, the trajectory of change may be determined and triggered by an external force such as a hurricane or a strong wind that causes a canopy gap to develop.

Adaptations in the forest that indicate responses to long-term effects of hurricanes, as well as to other disturbances, are: even and round tree canopies, uniform tree height, absence of tall emergents, rapid regeneration following soil disturbance or changes in microclimate, large number of standing dead trees, and the long-term behavior of the forests in terms of changes in species composition and in other structural and functional parameters (figs. 73, 74, and 98).

That the Luquillo Forest exhibits a decrease in species diversity over time and that this decrease is associated with hurricane frequency raises the issue of the role of disturbance in this forest. We assume that ecosystems under stress generally exhibit low species diversity, while those growing in unstressful environments increase species diversity over time. The former type of ecosystem is considered to be under allogenic (external) control, while the latter is thought to be under autogenic (internal) control. Is the Luquillo Forest then a stressed ecosystem? Are most ecosystems in fact driven by external forces which effects we fail to recognize because many of nature's forces like fires, hurricanes, or earthquakes, are events with infrequent periodicities?

Energy Flow

Another important aspect of forest dynamics in the Luquillo Mountains is the question of the ways these forests maximize energy flow in spite of being submitted to contrasting environmental conditions. We hardly have any information to address this question with any degree of confidence. But, a number of inferences can be made with the information gathered above. For example, tree growth was believed to be much faster in the tabonuco forest than in the colorado forest. Yet, our analysis suggests that, in the long term, both forests exhibit equal growth rates. The strategy of growth is what differs. Growth in the colorado forest begins slowly and picks up speed later, while in the tabonuco forest, growth starts fast but ends at a slower pace. Why these ecosystems exhibit contrasting strategies is not known, but the ultimate result appears to be the same in terms of average growth rate.

One could argue that each forest ecosystem must allocate a fraction of its energy resources to develop enough structure and adaptations so that energy flux per unit area is maximized to cope with the environmental uncertainties typical of its location in the Mountains. However, depending upon location, the potential to build structure probably changes and this results in forests with contrasting development. Presumably, the harsher the environment, the more extreme and energy expensive are the adaptations. Natural selection must then operate for those solutions that are the most efficient and still allow for full use of available resources while also protecting against disturbances. A number of ecosystem level functions that contribute to the success of the tabonuco forest in the Luquillo Mountains are suggested in figure 99. Feedbacks are shown between herbivores and foliage diversity, fruit eaters and plant germination, pruners and regulators of stem wood, decomposers and mineral recycling, and dry air and mineral flows to leaves in the top of the canopy. What this diagram implies is that the mix of plant and animal species in the tabonuco forest have developed a symbiotic relationship by which mineral cycles and energy flows are optimized within the limits of the available energy and material resources. This, in turn, demands a considerable energy expense in the form of respiration which, when compared to gross photosynthesis, balances out to a P/R of about 1. What are the balances in the other forest types? What are the nature of feedbacks and control mechanisms in these other forests?

In the dwarf forest, for example, insect herbivory is extremely high (25%) along with a large degree of plant and animal endemism. Are these the costs of pollination in that wet environment? The complexity of this ecosystem is augmented by the epiphytic organisms, the surface location of roots, and the high density of stems. How are these structural features contributing to energy flow? What is the respiration rate in this ecosystem? Why do roots consume 51% of gross production in the tabonuco forest and grow along the ground surface of the dwarf forest for a longer distance than the height of trees? Is this system a net exporter of organic matter?

The same questions can be asked for the palm forest where plant diversity is dramatically reduced, but the complexity of adventitious roots and anaerobic processes is obviously higher.

As already indicated, these questions cannot be answered with our current understanding. But, it is clear that long-term observations with an ecosystem perspective are needed if we are to make any progress. The secret of the Mountains can only be unlocked by studying the mountain in its totality for as long as is feasible.

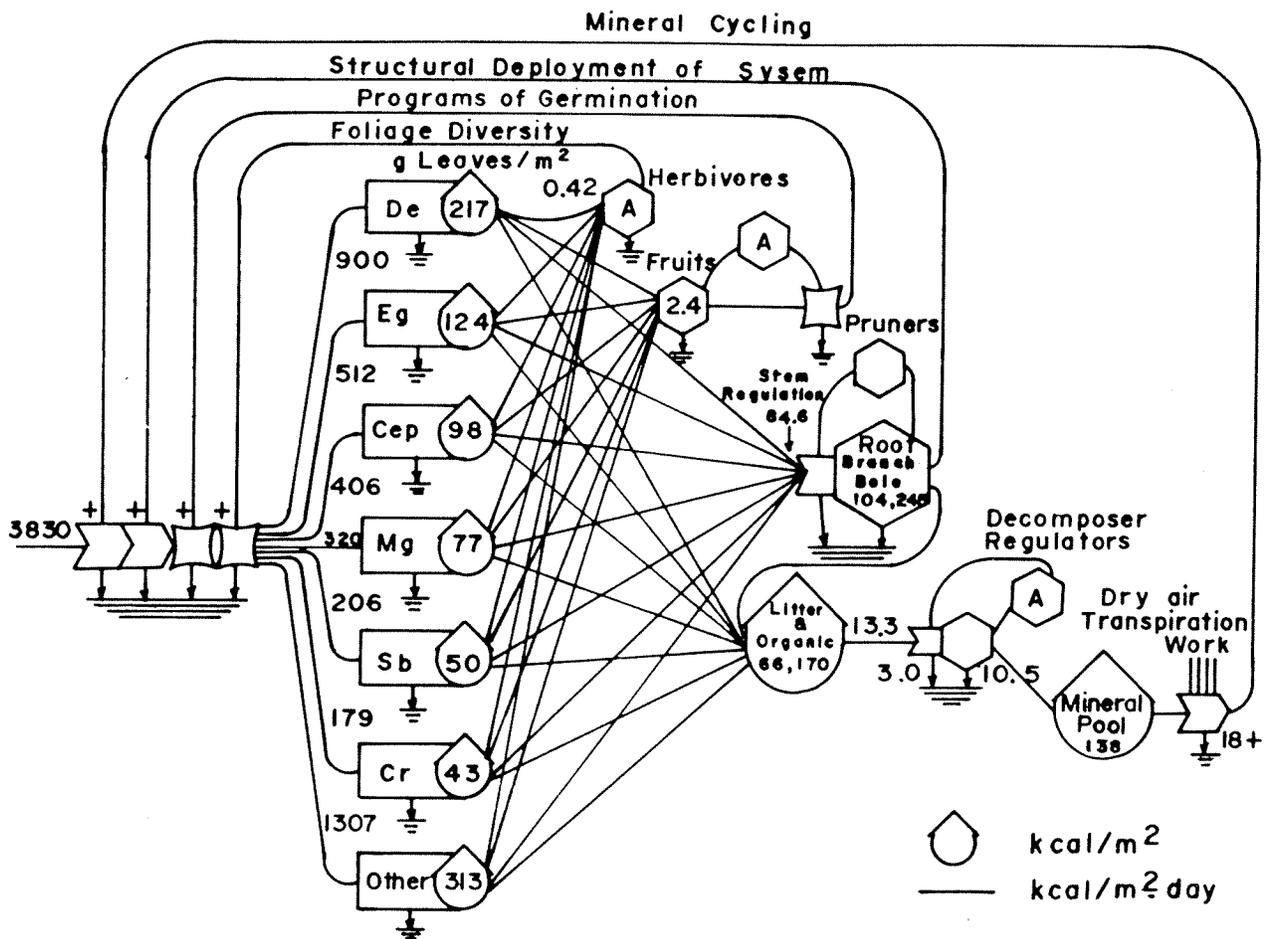


Figure 99.—Energy network diagram of the tabonuco forest at El Verde. De = *Dacryodes excelsa*; Eg = *Prestoea montana*; Cep = *Cecropia peltata*; Mg = *Micropholis garciniaefolia*; Sb = *Sloanea berteriana*; and Cr. = *Cirilla racemiflora*. (Odum 1970b).

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